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# Bulletin

*of the*

# Torrey Botanical Club

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# The morphological and cytological development of Meliola circinans

PAUL WEIDEMEYER GRAFF
(WITH PLATES 16 AND 17)

## INTRODUCTION

Our knowledge of the tropical fungi rests largely upon the foundation laid by the work of Berkeley, Bresadola, Cooke, Hennings, Léveillé and Rehm. At present, with the greater facilities at our disposal, closer contact with the region and better conditions for collecting, the number of workers on exotic fungi has been greatly augmented, and our knowledge of the tropical fungous flora is rapidly increasing. While the Perisporiales have been studied from the standpoint of their morphology and classification, but little cytological work relating to members of this order is to be found in the literature. Gäumann (1922) has studied the cytology of *Lanomyces tjibodensis*. A large gap remains to be filled in this very important phylogenetic position; namely, between the Erysiphales on the one hand and the Sphaeriales on the other.

The numerous papers on *Meliola* and related genera have dealt for the most part with descriptions of new species and varieties, though in some cases the studies have been pursued with an aim toward the modification and improvement of their classification. With the advancement and application of the idea that taxonomy should be an expression of phylogeny, more detailed studies are needed to supplement those of gross anatomy. In this way only can the niceties of distinction among the groups be brought out. This type of investigation often leads to the recognition as well of more fundamental facts regarding the life and habits of the organism.

In the development of this problem I have been concerned chiefly with the series of important steps included in the formation and growth of the ascocarp. Ward's (1883) conclusions regarding the rudiments of sex organs in *Meliola* were entirely hypothetical and inconclusive. In connection with this phase I have found that true sex organs are developed, and that, with the finding of these typical antheridia and oögonia, the ideas regarding the relationship of the Perisporiales with the Erysiphales become more firmly established. The prior formation of the hyphopodium, beneath whose protection these sex organs are formed, and its development into a hood-like stroma, that incloses all but the basal portion of the later-formed ostiolate perithecium with its protruding periphyses, substantiates the ideas of Bucholtz and Von Höhnel, though contrary to the prevailing notion in regard to this outer protective layer.

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Of no less interest is the parasitic nature of the species under consideration. Though haustoria have not been at any time observed, the evidence of parasitism is convincing, and this species is found to represent the extreme of ectoparasitism. It attacks the host epidermis with injurious effect without penetrating into the cell cavities or beyond the subsidiary cells at the stomatal opening.

The genus *Meliola* was first instituted by Fries (1825) with the species *Sphaeria? amphitricha*, based by him (1823) on three of Sprengel's (1820) species of the genus *Amphitrichum*. As first described this genus was placed by Fries in the "Sphaeriacei," but with the statement that it is somewhat analogous to *Erysiphe*. Later he (1830) strengthened his genus by the addition of a second species, *Meliola Psidii*, and nineteen years later (1849) transferred the genus to a new position, with *Erysiphe*, *Lasiobotrys* and *Asterina*, in his group Asterinei of the "Perisporiacei."

Bornet (1851) seems to have been the first to consider the structure of the members of this genus with other than a purely taxonomic viewpoint. He adds somewhat to the knowledge of their coarser anatomy, but contributes nothing in regard to their method of development or the formation of their ascocarps.

To date Ward (1883) has given us by far the most extended account of the development of *Meliola* and, in the confusion of ideas as to the morphology and classification of the group found in the later literature, his data are most constantly referred to, either directly or by implication. With regard to sexuality in this genus he arrives at certain interesting conclusions. He says in this connection, "The original pyriform branchlet —containing in itself, so to speak, the elements of the fruit-body—after the first division, may be considered as establishing morphologically an 'archecarpium' (De Bary, Beiträge IV, proposes to use this word as denoting that part of the body which becomes the ascus and pedicel in *Podosphaera*) and an antheridial branch—or the latter may be considered as containing in itself the antheridium, plus the elements of the perithecial wall." He looks upon *Meliola* and its allies as a branch group derived from the *Erysiphe* stem, either from ancestors of *Erysiphe*, or ancestors which gave rise to *Eurotium* and *Erysiphe*, and considers that these forms have developed in the tropics along lines parallel with the Erysiphaceae.

Gaillard (1891, 1892) believes that two sorts of hyphopodia can be readily recognized, and distinguishes them as "hyphopodies mucronées" and "hyphopodies capitées," for he says that all hyphopodia do not produce perithecia. The mucronate hyphopodia are considered as merely hyphal branches which have their development arrested. Ward made no distinction among the hyphopodia and believed all to be of this nature.

Growth may be resumed, as Gaillard says frequently happens, in which case one of the two opposite hyphopodia retains its habitual aspect while the other grows into a typical vegetative hyphal branch. Gaillard describes the presence of only a single protective wall about the ascocarp and fails to find any indication of an ostiole.

Thaxter (1896), speculating upon the nature of the Laboulbeniaceae, and their possible relationship with the Hypocreaceae and other pyrenocarpous Ascomycetes, says, "It is worthy of note that the bodies most nearly resembling the characteristic antheridial cells found in this family are the 'hyphopodies mucronées' of the *Meliolae*." This assumption is doubtless largely due to the influence of Ward and Gaillard, and is based on the conception that while the capitate hyphopodia may develop into ascocarps, the mucronate develop no further, and he infers for these latter the function of antheridia.

Fischer (1897) places the *Meliolae* under the Plectascineae within the Aspergillaceae, and in association with *Testudina*, *Zukalia* and *Ceratocarpia*. Bucholtz (1897) draws critical attention to Fischer's arrangement, and disagrees with his views on the structure of the members of this genus. A well developed ostiole was observed by him to be present at the time of maturity, though in the early stages of development none was apparent. Periphyses which protruded through the ostiole at the time of maturity were also observed, but no paraphyses were found. It was seen that the numerous periphyses within the ascocarp were colorless, while the portion of those exposed through the ostiole became much thickened and brownish in color. In the young condition, he says, in agreement with Ward, that the interior of the ascocarp appears to be of a true parenchymatous nature, and that within this parenchyma tissue there appears a cell rich in cytoplasm which seems to be the ascus anlage.

Von Höhnel (1917), in studying a number of the *Meliolae* and related forms, comes to the conclusion that the thyriothecium (Von Höhnel 1910) is not a single structure but composed of two portions, a protective shield and a true perithecium. He also finds that the perithecium is not inverted but upright in its development, thus agreeing with Gaillard (1893) on this point.

Arnaud (1918) is of the opinion that the hyphopodia are not functional as sexual organs, but says that they are rudiments of perithecia and organs of absorption, and proposes to designate the capitate hyphopodia as stigmopodia. He places *Meliola* in the Dothideaceae and considers that, from the point of view of the ascocarp and ascus form, they are much simplified and probably related to the Microthyriaceae through the Wardineae.

## MATERIALS AND METHODS

In the following investigation the material used, *Meliola circinans* Earle, growing upon *Carex* sp., was gathered by Professor R. A. Harper, in the vicinity of Miami, Florida and through his kindness furnished to me for study. The fungus, upon portions of the host, was fixed in the field, when gathered, in Flemming's medium fixative. As soon as practical this was embedded in paraffin so that up to this stage there was no delay in the sequence of preparation. In the further preparation of the material for observation sections were cut, and mounted in the usual manner, from 5 to 7.5$\mu$ in thickness, varying with the condition of the material, and feasibility of obtaining thin sections. Due to the hard outer covering of the fungous fruit and the heavy cutinization of the epidermal cells of the host, thinner sections did not prove practical. In staining the Flemming triple method was used as giving the greatest amount of contrast and clearness for observation.

Certain ambiguities have crept into the terminology employed in the discussion of the ascomycetous fungi. The term *ascocarp* is used throughout this paper to designate the entire ascus bearing fruit. In so doing, it is with the idea that the term is a general one applicable to any ascus producing fructification, of whatever type, whether apocarpous, pyrenocarpous or cleistocarpous, and also whether simple or compound.

The term *perithecium*, too frequently loosely used to designate the entire fructification, is here applied in a more restricted sense. Properly the perithecium is a product of the gametophytic stalk cells from which the sexual reproductive organs also develop, and is an inclosing protective envelope whose initiation is evidently closely correlated with the formation of these organs. The perithecium includes normally several layers, as pointed out by De Bary (1884) and Harper (1896, 1905) in their studies on the structure and development of the mildews, an outer cortex, when its functions are not usurped by a substituting tissue as seems to be the case with the Dothideales, and an inner nutritive layer in association with which may develop the paraphyses and periphyses.

Until the real relation of sporophyte and gametophyte in the ascocarp of the *Meliolae* and other Ascomycetes is clearly recognized certain general terms will prove useful. For the portion within, the term *core* as used by Ward (1883) seems better than "nucleus" or "kernel" sometimes found in the literature for denoting in a general way the portion contained within and bounded by the perithecium. In the same way it is frequently convenient to designate as *cortex* the portion of the ascocarp outside this core. When more specific distinctions are required the appropriate names for the various portions must be used.

## MYCELIAL DEVELOPMENT

*Meliola* is a genus of very wide distribution throughout tropical and subtropical regions of both the eastern and western hemispheres. Within this range a great number of species are found growing upon a wide variety of host plants, but almost entirely restricted in habitat to their leaves, and usually appearing upon these when they are in a mature or nearly mature state.

The vegetative development begins, according to Ward (1883), with the germination of any one or several cells of the pluricellular spore on the surface of the host. Following germination the hyphae spread in a diverging radiate manner over the leaf surface and form a dark incrusting layer, the maculae of Fries (1823) and Montagne (1842). Frequently, in the younger and smaller maculae, the remains of the initiating spore can be found in a central location. The evidence seems to show that each of these areas is the result of infection by a single spore, except in cases when numerous infections take place and adjacent growths become confluent. However, if it is possible for any one or even all of the cells of the spore to take part, the hyphae which compose a single macula may be the product of more than one of these cells. In view of the peculiar nuclear distribution within the developing spore, such as I have described in the following pages, and the condition found by Dodge (1927, 1929) to exist in the genus *Neurospora*, it would seem that further work and observation upon spore germination and nuclear activity in *Meliola* is very desirable.

Considering the presence of ascocarps as a sign of maturity, it is found that the maculae of *Meliola circinans* Earle vary from three to five millimeters, rarely more, in diameter. They have a slight tendency toward an oval shape due to a slight inhibiting effect of the raised longitudinal leaf veins upon the hyphal growth. In different species these maculae vary in size, regularity and form, and constitute the so-called subiculum in association with which the ascocarps develop.

Though ascocarps usually begin to appear on the maculae when they have reached a diameter of approximately three millimeters, they will occasionally be found on somewhat smaller spots. Their formation proceeds from the center outward. At the beginning of this period, in consequence, there is a margin of hyphae upon which they are not yet evident. With increase in size, and the accompanying maturity of a larger area, ascocarp production progresses outwardly in all directions. When a diameter of about five millimeters has been attained hyphal growth seems to cease, but ascocarp formation continues until they are at last found near the outer limit of the spot. One would judge from appearances that asco-

carp production continues at the center, as well as over the other portions of the maculae, for some time. Finally the center may be readily broken away while the marginal portion remains still quite firmly applied to the host. The character of the hyphae, method of branching, etc., are well known and need no detailed description.

Besides the usual type of branching, sterile, rigid, simple or branched hyphae, the familiar upright setae, may be produced from various portions of the vegetative growth. In some species these are found more numerous about the base of the ascocarp and in many cases irregularly disposed upon its surface. In our species they appear scattered upon the vegetative hyphae, as simple, straight, upright branches that taper to an acute point and measure from 400 to 800$\mu$ in length and about 12$\mu$ wide at the base. Only rarely have they been found to make their appearance upon the surface of the ascocarp (fig. 9), nor are they at all numerous about its base. This latter condition is undoubtedly correlated with the absence of a well formed hyphal cushion or "hypothecial disk" such as is usually more or less pronounced beneath the ascocarp in species where basal setae are numerous. Bornet (1851) figures these setae in such numbers and regularity about the base of the ascocarp as to emphasize the Friesian idea of their similarity to the appendages of the Erysiphaceae, particularly in the case of *Meliola furcata* Lév., where the ends are ornately branched much as in *Microsphaera*.

More or less regularly arranged short side branches also develop in large numbers. Each consists at first of a small stalk cell and a slightly enlarged end cell. These are the familiar hyphopodia, or morphologically arrested branches, and partake of the nature of appressoria. It seems that, partially at least, nourishment is obtained through their agency. Their under surface is thin-walled and in close contact with the surface of the host. Further than this these hyphopodia are directly associated with ascocarp formation and the reproduction of the fungus.

The hyphopodia are potentially capable of further growth though the great majority do not develop beyond the condition just described. Setae may develop by their upward prolongation. Renewed growth in the original direction may take place and result in ordinary vegetative hyphal branches. If, however, the terminal cell enlarges somewhat and the first septation is diagonal and is followed with an increase in the number of cells by meristogenous development we have formed the capitate hyphopodium of Gaillard and the anlage (figs. 1, 2) of an ascocarp. I find no occasion for a morphological distinction between types of hyphopodia other than one of ultimate development.

Hyphopodia notably similar in position, development and function

have also been described by Doidge (1920) for the related genus *Amazonia*, under the name *Meliolaster*, as well as by Stevens (1927) for *Irene*, *Irenopsis* and *Irenina*.

## HOST RELATIONS

The encrusting type of growth developed by the *Meliolae* upon the leaf surface of a vast number of tropical and subtropical plants raises the question as to their saprophytic or parasitic habit and relations to the host substratum. It has never been adequately shown whether they are primarily saprophytic and dependent for their food supply upon materials accumulated from the air or excretions of leaf infesting insects, or, if parasitic, the extent of their parasitism and the amount of injury they may cause.

It has been generally assumed that the growth upon the leaf surface including the so-called subiculum associated with ascocarp production, constitutes the vegetative stage. This incrustation is, in many cases, easily separable from the leaf surface upon which it may be thriving, while in others separation seems to be accomplished with more difficulty. The xerophytic nature of the fungous crust, composed of heavy-walled hyphae, except that at the time of growth they remain lighter at the tips for a brief period, would seem to preclude the assumption of any active attack on the leaf surface. The literature contains but meagre reference to the ability of superficial fungi, or any others, to attack heavily cutinized cell walls. The entrance of haustoria or penetrating hyphae through this protective layer has been, however, much studied.

Bornet (1851) questions the real parasitic nature of *Meliola*, and is of the opinion that the lesions, observed occasionally on the leaves upon which it is found growing, are due to the action of numerous mites whose remains one often finds. With this Gaillard (1892) agrees, and adds that by examining numerous leaf sections he has satisfied himself that the *Meliolae* are entirely superficial, and do not in any way injure the tissues of the plant upon which they grow. Berkeley (1857), without direct evidence, is very positive as to the injurious effect of the fungus on the host.

Ward (1883) says that on the under side of the hyphal wall, where in contact with the host, thinner spots, lacking coloring matter, will be seen where the protoplasm is more nearly in connection with the outside. These bright spots are the points of attachment to the epidermis, and may be regarded as haustoria of a very rudimentary nature.

In all, Maire (1908), Arnaud (1914, 1918) and Doidge (1921) have demonstrated the presence of haustoria in sixteen species of *Meliola*. In

two of these the haustoria penetrate to subepidermal cells in the same manner as do those of *Asterina*, though remaining simple and unbranched. The fungus was found to be easily separable from the host in the case of *M. bifida* Cke., and Doidge was unable to show the presence of haustoria in connection with this species. Ward found no evidence of haustoria in the unnamed species of *Meliola* which he investigated, though he (1882) had no difficulty in clearly demonstrating their presence in *Asterina spisa* Syd., at an earlier date. Gaillard says that after examining numerous leaf sections he has satisfied himself that the *Meliolae* are entirely superficial, but he does not name the species he sectioned.

In *Meliola circinans* Earle I have found no evidence of the presence of haustoria, and the fungus is to all appearances entirely superficial. The hyphae are in intimate contact (figs. 1, 4, 7, 8) with the epidermis and follow closely all its irregularities. Also the cell walls of the hyphae are seen to be markedly thinner wherever this contact is maintained. Stomatopodia (fig. 4) may enter and fill the deep cavities within which the stomata are located. This plug or foot, however, does not pass between the guard cells, but terminates at this point where it is in contact with them. It develops no further, and no fungal growth appears in the substomatal cavity. As pointed out by Theissen (1916) for *Stomatogene* (*Dimerium*) *Agaves* (Ell. & Ev.) Theiss., where a similar situation occurs, we have the natural question as to whether the fungus should be considered as superficial (oberflächlich) or as really penetrating (eingewachsen) the host. In view of the form of the plug in this species of *Meliola*, which is indented at its base immediately over the stomatal opening but closely appressed to the outer walls of the host cells, it appears that a purely superficial relation must exist between fungus and host.

Where the fungous hyphae and host are in contact it is seen that, coincident with the hydrolysis of the heavily cutinized wall, the first change to appear is a slight swelling accompanied by an irregular reduction in staining capacity (fig. 4) of the host wall, thus showing evidence of a chemical as well as physical alteration. This is followed by evidence of digestion which results in the irregular thinning (fig. 8) of the host wall. While the swelling which takes place is very slight, the succeeding reduction in thickness is well marked, with the hyphal filaments of the parasite closely fitted into all resulting depressions and irregularities.

We have then, from the evidence at hand, three grades of parasitism represented in the genus *Meliola*. Most frequently haustoria of a simple type are formed. They penetrate the cuticle of the host and form an haustorial vesicle in the cavity of the epidermal cell. There are occasional species which develop haustoria of the *Uncinula salicis* type (Smith,

1900) which, though still simple unbranched structures, penetrate to the cell cavities of the mesophyll region. And lastly there are species, wholly superficial in character, which fail to come into direct contact with the host cytoplasm, but in some way corrode the epidermal cell walls more or less and, from the evidence of degeneration products (fig. 8) which appear within the epidermal cells, cause some real though not deep seated injury to the host. This corrosion process may be effected by any portion of the fungous hyphae in contact with the cuticle.

## ASCOCARP INITIATION AND DEVELOPMENT

As pointed out above, the ascocarp is the entire ascus fruit whereas I shall use the term perithecium to signify structures having the same origin as the envelope in the cleistocarpous Erysiphales. In the genus *Meliola* the ascocarp initials are first seen as short two-celled lateral branches growing from the sides of the vegetative hyphae to which Gaillard (1891) has given the name of hyphopodia. As previously noted Gaillard considers these hyphopodia to be of two sorts which he distinguishes as "hyphopodies mucronées" and "hyphopodies capitées." In this he has been followed by Thaxter (1896) and Gäumann (1926), as well as a number of systematists who use the characteristics of these two stages of development in species diagnosis. That these hyphopodia are equivalent to one another, as far as early development is concerned, there seems to be no doubt, though it is true that many of these structures seem destined never to develop further than the two-celled condition, and that but a proportionately small number are capable at any one time of developing into ascocarps.

The hyphopodia of the species under consideration are typically two-celled at the time of their early development. The enlarged rounded terminal cell is attached to the hyphal branch from which it originated by a single short stalk cell. This characteristic seems fairly constant for the genus, though this stalk cell has been reported as sometimes lacking. The terminal cell of the hyphopodium is in close contact with the surface of the host and, as previously suggested, may have the nature of a rudimentary appressorium. Those which continue development seem to have in many cases an association with the stomata of the leaf, and after reaching some greater size produce a foot or plug (fig. 4) which fills the epidermal depression between the subsidiary cells but not the guard cells. This plug does not penetrate the stomatal opening nor does it produce hyphal branches for this purpose. Apparently it serves only to secure a better contact with the surface of the host.

When it develops further as the anlage of an ascocarp, the initial

growth of the hyphopodium takes place in a centrifugal manner parallel to the plane of the leaf, and results in the formation of a lenticular group of cells. The first division of the terminal cell of the hyphopodium, as described by Ward (1883), takes place by the formation of a septum vertical to the plane of the mycelium and leaf and passes diagonally across the cell with a slight curve. Due apparently to the nature of this first septation, growth for a time results in a disk or plate with a subradial-subhelicoid appearance which, however, is soon lost as development proceeds. The exposed cell walls are thickened and dark colored in a manner similar to the walls of the regular hyphae. The vertical walls are heavy and colored for only a short distance below the exposed surface (figs. 3, 4, 5) and become rapidly as thin and colorless as the lower walls. This peltate stromatic growth is a purely vegetative structure, the formation of which undoubtedly takes place in the manner described by De Bary (1884) as meristogenous, rather than symphogenous.

In *Meliola* ascocarp initiation is not synonymous with perithecial initiation, and the latter does not begin till the growth of this stroma, as I shall class it, has proceeded far enough to produce a protective cover beneath which further developments take place.

Ward expressed the view that the initiation of the fruit structure of *Meliola* came about through a fusion, or at least a contact, of the first two cells formed by the hyphopodium. One of these he considered as having the nature of the "archecarpium" of De Bary, being the anlage for the inner structures including the ascogonium and asci. The other he believed to be the anlage for both antheridium and perithecial wall. Thaxter (1896), as previously noted, speaks of the "hyphopodia mucronées" as resembling the antheridial cells found in the Laboulbeniaceae. This statement seems to carry the implication that he considers Gaillard's (1891) mucronate and capitate hyphopodia to be the two sex organs, or at least to have in some degree their function. Ryan (1926) follows the ideas presented by Ward.

I find that under the protection of the young stroma, which is peltate in this early stage, two short stalks arise from the side adjacent to the original stalk cell of the hyphopodium. One of these is antheridial in its nature while the other is oögonial. These (fig. 3) are the true sex organs. They are definitely of the nature described by De Bary (1863) and Harper (1895, 1896, 1905) for *Sphaerotheca*, *Erysiphe* and *Phyllactinia*, the only difference being one of orientation, and in the size of the antherid which is longer. They are usually found growing in a position parallel instead of perpendicular to the leaf surface. This is due to their point of origin and relation to the shielding hood of the stroma. Rarely they tend to assume

an upright position when the curvature of the protective stroma is such as to allow them sufficient space.

Oögonial and antheridial development seems to take place simultaneously, and the branches from which these organs are derived have a point of origin very close to one another. The stalk cells from which the sex organs arise are much shortened, their breadth being greater than their length. From its short stalk the oögone develops as a much enlarged, oblong-oval cell with a single large nucleus and a dense protoplasmic content. The antherid is slightly longer, more slender, nearly cylindrical, uninucleate, and has a slight tendency toward a spiral form. The sex organs of *Meliola* are Erysiphaceous in character, but protected, as described, by the small peltate hood. Thus the oögone and antherid are closely associated in origin as in the Erysiphaceae, and, as the young stromatic growth is attached to the vegetative hypha by a single stalk cell, the *Meliolae* must be necessarily homothallic.

The perithecium begins its development by the growth of hyphae from the stalk cell immediately below the oögone. These hyphae also grow in a horizontal direction, at least in their early stages, following the general oögonial contour. Certain of them may originate from the stalk cell of the antherid, but these if present are clearly not so numerous as the others. Due probably to the fact that a protective cover is already present, these hyphal filaments do not form the intimate contact with the oögone during their early development that has been described for members of the Erysiphaceae.

To accommodate the growth of antherid, oögone and perithecium the overgrowth of stroma increases and assumes at this period a hemispherical form. Up to this time the stroma is usually but one cell in thickness, but at this period or shortly after, as shown (fig. 4) in median vertical sections, this growth increases to a thickness of two cells by the formation of an inner layer. At the side opposite the hyphal connection, where it is in close contact with the host, the stroma becomes three or four cells thick. This extra thickening projects inwardly toward the basal center of the ascocarp. As growth proceeds this basal stromatic thickening is extended around the entire ascocarp, and with the ascogenous tissue as a center tends to change the orientation of the latter. At no time, however, does this stromatic ingrowth entirely close together beneath the ascocarp, and the stroma retains its flammeaceous form from now up to the time of ascocarp maturity. At the basal center the thin-walled perithecial cells are at all times in contact with the host.

With the increase in size of the ascocarp greater space is provided for the developing perithecium and ascogonium through the intercalary

growth of the stromatic hood. This is accomplished, however, without any material change in the thickness of the stroma. The ascogonium elongates (fig. 4) as a horizontal filament, and becomes divided into a short structure of uninucleate cells. The terminal of these retains for some time the shape of the oögone but, as growth proceeds, is gradually reduced in size. After attaining a length of three or four cells, the ascogenous hyphae begin to make their appearanace as side branches. The first to develop grows from the penultimate cell of the ascogonium while the second seems to be usually the product of the third cell. Both grow from the distal ends of the parent cells so that the ascogonium, with the young ascogenous branches, has the appearance of a young hyphal shoot with a large terminal cell. Whether this large cell is capable of further growth, or whether more than two of the ascogonial cells produce branches, I am uncertain.

The cells of the core at this time are relatively large, and, being compressed in their rapid growth and confined position, assume somewhat of a pseudoparenchymatous appearance, particularly (fig. 5) when observed in cross section. During the young stages the ascogonium and ascogenous hyphae occupy a central spherical region. Their cells are all uninucleate, except as nuclear division involves a temporary increase. I have not found stages showing nuclear fusion in the oögone, nor nuclear migration from the antherid. The nearest approach to this latter phase that I have seen is an oögone (fig. 3) containing apparently a fusion nucleus and an associated antherid within which the most careful focusing of the microscope failed to reveal any sign of a nucleus.

At the same time the ascogonium is developing the perithecial structure is also continuing its growth about the inner surface of the, now flammeaceous, stroma. The cells of the outer perithecial wall, which is the first to be formed, appear in longitudinal section more slender and elongate (fig. 6) than those of the other structures, and its completion is rapid. A comparison of tangential and radial sections shows that the cells of this perithecial wall become flattened in much the same manner as those of *Phyllactinia* described by Harper, and have a similar appearance to them except that their walls remain unthickened. The development of the inner perithecial layer follows closely upon that of the outer. This also has its origin in the base of the perithecium, and its growth is directed upward about the sides of the increasing cavity. The cells of this layer, unlike those of the outer, are large and more nearly isodiametric. They are rich in cytoplasmic content, and variable in the number of their nuclei.

From a position slightly over half way up the inner portion of the perithecium (fig. 9), and upward toward the apex, branches, the periphyses, are produced from the inner layer and grow across the upper por-

tion of the cavity. Their ends meet and overlap somewhat, with the result that this region is more or less occupied for a time. As this growth has been taking place, the ascogenous hyphae have continued their development over the inner base of the perithecium. Branches from these grow upward and begin the development of the first asci. Among these first asci to be formed there are seen also a few scattered paraphyses which have their origin in the perithecial base. The ascogenous hyphae are uninucleate, and the asci develop from the penultimate cell (figs. 10, 11) through the typical crozier stage. The first few to appear remind us of Ward's description for they are seen as cells which "maintain their large size and upright arrangement" in the central part of the core. They are undoubtedly the same as the cells seen by Ward (1883) and considered by him as constituting the ascogonium.

There are seldom more than two or three mature asci to be seen in any one section of an ascocarp, but numerous and varied early stages are also present showing that their production must continue for some time. The growth of the comparatively large asci with their large spores has a marked effect upon the entire inner structure of the ascocarp. With the increased spread of the ascogenous hyphae and the attendant ascus development, the inner perithecial layer becomes much flattened until its cells appear in section as a thin layer of shrunken, elongated cells poor in cytoplasm. The entire perithecial structure seems to serve as nurse tissues, and to become more and more compressed as development proceeds. The draft of material for nourishing the ascogenous hyphae and the developing asci may even extend in some degree to the inner stromatic layer. Thus all parts of the ascocarp cortex, except possibly the outermost protective layer of heavy walled cells, may contribute to their maintainance and growth, and serve in a sense as nurse cells.

Paraphyses make their appearance during early ascus formation, and are present (fig. 9) from that time through the active life of the ascocarp. At no time, however, are they numerous but remain few and scattered among the asci. They are never straight and regular in their arrangement, but grow upward as slender unbranched, twisted and bent filaments of several cells with thin walls throughout their length. In those that appear oldest the cytoplasm is very irregular in its staining quality and the size and distribution of its vacuoles. The nuclei of these are elongated and appear to be in a state of degeneration. In contrast, the younger newly formed paraphyses have a homogeneous cytoplasm and normal, spherical or slightly ovate nuclei.

As the ascocarps increase in size and the central cavity enlarges, the filaments growing into the upper region from the inner wall of the peri-

thecium become more slender. Where they formerly overlapped they now show signs of separation. This takes place first in their basal region and progresses upward. As this separation continues (fig. 9) these filaments, the periphyses, all tend to become directed upward toward the apex of the ascocarp. Those reaching farthest upward push apart the cells of the perithecium and stromatic hood at this point. The tips of the periphyses then protrude, and their terminal cells substitute (fig. 17) for the displaced portion of the stroma. The exposed ends become rounded, slightly enlarged and develop thicker, dark-colored walls which match well, except in size, the outer walls of the stromatic cells. This condition undoubtedly accounts for previous failures to observe the protruding periphyses. Ward observed, in an unnamed species of *Meliola*, a slight papilla at the apex of the ascocarp. He also noted that the cells of the inner wall converge toward this spot, and concluded that this is at least a weak point through which spores escape. Bucholtz (1897) found that in *Meliola corallina* Mont., *M. amphitricha* Fr., and *M. cymbisterma* Mont., there is a well developed perithecial ostiole from which periphyses were seen to protrude at the time of maturity. Aside from these statements of Ward and Bucholtz we find no direct reference to ostiolar development in the extensive literature on this genus.

With the approach of complete maturity, the perithecial cells at the base of the ascocarp, where unprotected by stroma, and in contact with the host, develop thickened walls. These are nearly as heavy and dark colored as those of the exposed stromatic layer. At the same time the ascogenous hyphae have increased so that they are distributed over the enlarged base of the cavity. With this growth they have become more slender, and the various stages in ascus formation appearing in each section are more numerous. Paraphyses are still to be found sparsely scattered among the asci. In the upper portion of the cavity the periphyses are seen to have lost much of their original protoplasmic content and to become more consolidated into a crown or cap of hyphae converging toward the apex of the ascocarp. The formation of this perithecial ostiole as a definite place of dehiscence is in agreement with the findings of Bucholtz. That the ostiole does not attain complete development until the first formed asci are approaching maturity and nearly ready for the discharge of their spores is also in harmony with his observations.

### ASCUS AND ASCOSPORE DEVELOPMENT

During early ascus development the hyphae from which they originate are short and composed of cells with a relatively large diameter and a single, prominent, though not large, nucleus. The first few asci to appear

form a group of large, upright cells occupying the center of the ascocarp. These have developed from the first-formed, short ascogenous hyphae seated upon the portion of the inner perithecial wall at the base of the ascocarp. From the cells of this wall, which are quite large at this period, a few scattered paraphyses are found growing upward among the asci, and of about the same length. The asci pass through the typical crozier stage (fig. 10), in their early development. The ascogone becomes unrecognizable among the growing hyphae during this early period.

During the later growth of the ascocarp the removal of reserve materials results in the somewhat diminished thickness of the perithecial wall and this, together with the increased size of the fruit body, serves to increase the size of the inner cavity. At the same time the developing asci are brought, as a consequence, into a relatively lower position. The ascogenous hyphae, in continuing to spread over the enlarged ascocarp base, become more attenuated and their branches more numerous, intertwining and difficult to follow. With the smaller diameter of their cells, their nuclei are also slightly diminished in size. Under this condition, however, as the crozier is being formed, the three or four cells nearest the end of the hypha so engaged increase in diameter, and the nucleo-cytoplasmic ratio is maintained by a concurrent increase in the size of the nuclei. It is thus seen that the continued production of relatively large asci is not dependent entirely upon growth after ascus formation, but is related in some degree to a stimulus present within the hyphal filaments at the time of ascus initiation.

The crozier is formed in the usual manner, and after the enlarged, broadly ovoid ascus cell becomes (fig. 11) two to three times longer than broad, and about one forth the length of a mature ascus, its two nuclei fuse. The fusion nucleus is very large, and shows evidence of a considerable growth before the first division takes place. It occupies a position near the center of the ascus and attains a size approaching two thirds the diameter of that cell. The cytoplasm is homogeneous throughout the entire ascus.

As the ascus elongates and becomes clavate in form the first nuclear division takes place, and this is soon followed by the second and third divisions. As is the case with many ascomycetes, the first division takes place in the general direction of the long axis of the ascus, or in a slightly oblique manner. The two daughter nuclei remain near the center where the second division also takes place. In this the direction of division is oblique, and the four nuclei, still retaining a central location, prepare for the third division. The resulting eight nuclei, in remaining likewise in the central portion of the ascus, make it difficult to trace their relationships to one another.

Though, ordinarily, but two spores (fig. 14) are found in the mature ascus, the usual eight nuclei are to be seen prior to spore formation and all take part in early spore development. Following the last nuclear division there is an arrangement of the nuclei in pairs, in such a manner that if median transverse sections of an ascus are seen but four would be in the field at one time. While in this position the four spores are cut out.

In Ward's description of spore formation no mention is made of nuclear conditions. According to him the procedure is a progressive one in which the first act is a longitudinal cleavage dividing the ascus content in half. This, he says, is followed by a second cleavage, likewise longitudinal, but at right angles to the first. With this my observations do not agree for I find that the spores are cut out simultaneously as four fusiform cytoplasmic bodies. These each contain two of the eight nuclei (fig. 12) located in a median position. In the act of spore delimitation the greater portion of the cytoplasm is included within the spores, and only a very small amount of residual epiplasm remains in the ascus. Throughout ascus development the entire cytoplasmic content remains very homogeneous, and there are no largely vacuolated regions such as are common in those species that produce proportionately smaller spores and a larger amount of epiplasm.

In the delimitation of the four spores within the ascus, instead of the usual eight, together with the cutting out of the cytoplasm so as to include two of the eight nuclei within each spore, we are reminded of Wolf's (1912) first report of such an occurrence where he describes a similar condition for *Podospora anserina* (Rabh.) Winter. The next to bring to our attention a like feature is Dodge (1927) who found that in *Neurospora tetrasperma* Shear and Dodge, the cutting out of four binucleate spores within the ascus is the normal event. To these may be added the variation which Dodge (1928) later reports when he says that in *Keithia Chamaecyparissi* Adams, the two spores of its asci are each cut out with four nuclei. In other cases, so far investigated, where fewer than eight spores are regularly formed, such as that of *Phyllactinia corylea* (Pers.) Karst., investigated by Harper (1905), *Verpa bohemica* (Krombh.) Schröt., by Komarnitsky (1914) and *Laboulbenia chaetophora* Thaxt., and *L. Gyrinidarum* Thaxt., by Faull (1912), it has been found that some of the nuclei degenerate prior to spore delimitation and only those retaining their normal size take part in spore development. In these latter the usual uninucleate spore is formed and the degenerating nuclei gradually lose their identity within the epiplasm.

When the spores are first formed in *Meliola circinans* Earle, there are four in each ascus (figs. 12, 13, 14) but as they proceed in their develop-

ment two of these grow in size at the expense of the other two. As first cut out the four spores are of equal size. The growth of two of these is rapid, while at the same time the other two diminish laterally and become thinner as the others become larger. Finally only two remain, the last trace of the others having disappeared. Though I have seen instances where all four spores of an ascus have completely matured, such occasions are very rare. I have never found cases where numbers other than two or four develop.

The individual spore (figs. 14, 15, 16) in our species is five-celled at maturity, and at this stage always contains six nuclei, two in the middle cell and one each in the others. This nuclear number is arrived at through normal division and without the loss of any nuclei by degeneration. The formation of the several spore cells and their nuclei is achieved by a progressive development. After the simultaneous division of the two nuclei in the young single celled spore the four daughters become arranged in a median line, one from each pair approaching the end of the spore nearest to it. The remaining daughter nuclei retain a position near the center of the spore in about the same location as their parents. Just prior to the next nuclear division the end cells of the spore are formed by the development of cross partitions. In this way a single nucleated cell appears at each end of the spore, and a very large binucleated cell is left in the center. The nuclei of the terminal cells do not divide again during spore growth. The two nuclei of the large central cell, which is destined to develop into the three that remain to be formed in the spore, then both divide (fig. 15) in a diagonal direction. With this division the formation of the six nuclei of the mature spore has been achieved. Two walls are then formed cutting off the second cell from each end with single nuclei and leaving two nuclei, granddaughters of each of the original, in the central remaining cell.

I have also seen sufficient evidence to lead me to conclude that a reversal of the above mode of spore septation may take place, and that in this event daughter nuclei of original nuclear pair will be present in the central cell instead of their granddaughters. This seems more likely to occur when the spore breadth develops at a proportionately greater rate than its length. In this event the original pair of nuclei divide diagonally, and with the cutting off of the central cell, which in this case is the first one formed, a daughter of each is included. As the spore continues to elongate the other two nuclei then divide, move into alignment and are then separated from one another by cross partitions. In this way the two cells toward one end will have single nuclei that are granddaughters of one of the originals while the two toward the other will have single nuclei that are granddaughters of the other of the original pair, and the center cell will contain two nuclei, a daughter of each member of the original pair.

As the two spores of the ascus increase in size their adjacent sides are somewhat flattened by pressure, and the nuclei (fig. 14) of each become arranged in a line on the side of the spore away from its neighbor. With continued growth each cell of the spore becomes somewhat rounded, resulting in a slightly constricted appearance at the location of the transverse walls. The terminal cells become obtusely rounded or slightly apiculate. As the condition of maturity approaches the cell walls (fig. 16) become much thicker and dark colored. This dark brown color of the mature spore becomes so dense as to obscure almost completely the cytoplasmic content.

The ascus wall is thin at all times, and, as the spores develop, becomes distended and fits closely about their contour. It readily tears away at the base when mature, and often continues to invest (fig. 14) the paired spores for sometime. These may be seen in the ascocarp cavity ready for discharge and covered by the remnant of the ascus wall that is so thin as to be barely visible. On breaking or tearing in any other region the spores escape and separate in the cavity leaving the fragile collapsed ascus behind.

Ordinarily the spores are discharged through the perithecial (fig. 17) ostiole. As the older fruits may break away from the substratum and the base of the ascocarp is unprotected by the stromatic growth, instances are not rare where the exposed perithecium by breaking allows the spores to escape through the more lightly protected base. This condition is, in all probability, the explanation of Bornet's conclusion that normal dehiscence takes place by the formation of a circular rupture about the base of the ascocarp, and that the top and sides of the "concepticle" serve as a lid.

## DISCUSSION

The historic basis in the classification of the Ascomycetes has naturally been to a large extent one of gross morphology. With the increased study of the more minute details of structure, cell fusion and nuclear behavior connected with their life history, the finer distinctions in the evidence for phylogenetic relationships have gradually emerged. In the genus *Meliola* we find for the first time among the Perisporiales the true oögone, as originally described by De Bary for the Erysiphales. This organ as I have shown in the present paper, appears as an enlarged uninucleate cell, beneath the protective stromatic shield, in close association with a more or less spirally twisted antherid. It is usually, though not always, seen growing in a position parallel with the surface of the host. This orientation is due, in part at least, to the confinement of these organs beneath an incrusting stroma. Hyphal branches grow from the stalk cell bearing

the oögone, develop much as in the Erysiphaceae, and surround that organ. A perithecium is produced in the same manner as has been reported for *Erysiphe*, *Phyllactinia* and *Sphaerotheca*, except that it matures into a true ostiolate structure rather than a cleistothecium, and is located under a thin flammeaceous stromatic layer whose cells are pushed aside to allow the ostiole to become exposed and the periphyses to protrude.

Harper (1905) mentions the occasional presence in the young ascogonium of *Phyllactinia corylea* (Pers.) Karst., after fertilization, of a small nucleus whose fate he was unable to determine. This was but one-third the diameter of an ordinary nucleus, or even less. The suggestion is made that possibly the first division in the oögone may give rise to a supernumerary nucleus similar to that found in the germination of the zygospore of certain algae. A similar nucleus has since been observed and figured by Winge (1911) in the oögone of *Sphaerotheca Humuli* (DC) Burr., but prior to migration of the male nucleus. As shown in his figures, one of the two thus formed enlarged to become the oögonial or egg nucleus while the other becomes reduced in size. Whether these small nuclei of Harper and Winge are identical must be considered at present uncertain. Their position and degeneration would seem to indicate that such is the case. The fact, however, that in one case this nucleus was found subsequent to fertilization while in the other it is reported as found in the unfertilized egg may cause some feeling of doubt.

I have found a similar small nucleus located below the large fusion nucleus in the female sex organ of *Meliola*, and, from its appearance, undoubtedly in the process of degeneration. In view of the phylogenetic development of the Ascomycetes, and the reduction of the archicarp to the single celled oögone, it seems not improbable that this superfluous nucleus can best and most simply be accounted for as vestigial. It seems not at all unlikely that in the development of the short oögonial filament, when the terminal cell increases in size, nuclear division may sometimes take place. As no cross wall is formed, the oögone begins its development with two sister nuclei one of which becomes functionless and degenerates while the other serves as the active nucleus of the egg. In those forms in which the archicarp possesses a trichogyne and conductive cells beyond the egg cell such development is carried even further and is accompanied by septation. With the reduction of this organ it is not unnatural that at times supernumerary nuclei may be found. Dr. Illo Hein tells me that in his studies (1927) of *Sphaerotheca Castagnei* Lév., he found a similar degenerating nucleus sometimes present in the female sex organ. The length of the trichogyne and extent to which the conductive cells are developed appear to be a matter of ordinary growth and to depend on the ecology of the fungus.

In a similar way we can also account for the controverted nucleus found by several workers in the trichogyne of certain Florideae. In those cases where a trichogyne is present, whether in the Florideae or Ascomycete, its nucleus or nuclei degenerate after passage of the male nucleus and not before.

With the removal of a considerable number of genera from the ranks of the Perisporiales this seems to be gradually becoming a depauperate order. Apparently these revisions are due, in part at least, to the recognition of the presence of an ostiole in an accumulating number of species. For example, this together with other factors led Arnaud (1910) to remove to the Sphaeriales such genera as *Limacinia*, *Capnodium*, *Perisporium*, *Zuklia*, *Meliola*, *Asteridium* and several others from their old position.

Theissen (1913, 1917) has instituted a new order, the Hemisphaeriales, to receive genera largely Perisporiaceous in their nature. These views have been accepted in part by Gäumann in his "Vergleichende Morphologie," as well as by C. W. Dodge in his revised translation of that work. They have both allowed *Meliola*, however, to remain in its old position among the Perisporiales. Later Arnaud (1918, 1925) revised his earlier conclusions and has suggested the removal of *Meliola*, together with *Amazonia* to the Dothideales. While it may seem expedient to divide these numerically rapidly increasing groups, the recent subdivisions seem to be the cause of unnecessary confusion. Either the members of the Perisporiales should be entirely distributed among other orders or the definition and boundaries of this order should receive a much needed emendation. The question is one of phylogenetic conception.

Much of the confusion of the past is found to hinge upon a misconception of what constitutes a perithecium, and the loose use of that word in reference to the outer portion of an ascocarp when a stroma is present. The genus *Meliola* offers a good illustration as few species descriptions appear in which the outer fruit surface is not designated as the perithecium, though in reality it is the surface of a flammeaceous stroma beneath which the perithecium is hidden. Setae appearing upon the surface of this ascocarp are spoken of as "perithecial setae." As they are outgrowths from the stromatic surface they must have the same general origin as the hyphal setae, and to speak of them as perithecial setae gives a wrong impression. The setae of *Meliola* may be produced from strictly vegetative hyphae, from its hyphopodia or from the stromatic surface of the ascocarp, and in some species they are developed from all three localities. All are vegetative in their origin. In spite of the similarity in appearance, the ornately branched setae of *Meliola furcata* Lév., which appear

about the ascocarp, have their origin in the stroma while those of *Microsphaera* are outgrowths from a true perithecial wall. The latter have their ultimate origin in the stalk cell of the oögonium which produced this perithecium.

Between *Meliola* and the genus *Asterina*, which Theissen places in the Hemisphaeriales, we find *Amazonia* with, as pointed out by Doidge (1920), intermediate characteristics. This latter genus is associated with *Meliola* in the Meliolineae by Stevens (1927), classed among the Hemisphaeriales with *Asterina* by Theissen and Sydow (1917), and among the Dothideales, together with *Meliola*, by Arnaud (1918). Theissen based the genus *Amazonia*, on *Meliola asterinoides* Henn. That these three genera, *Meliola*, *Amazonia* and *Asterina*, are without doubt very closely related to one another is shown by their development, and emphasized by this lack of uniformity in agreement with regard to the proper position for *Amazonia*.

The chief distinction between *Meliola* and *Asterina*, in the morphology of the ascocarp and exclusive of such details as spore character, lies in the fact that the development of the ascocarp in the former is by epinastic growth while in the latter the growth is hyponastic. In *Meliola*, though the ascocarp at its start is a flattened structure, on approaching maturity the upward development to accommodate the large asci in fasciculate arrangement results in a spherical fructification with an enveloping hood-like or flammeaceous stroma. In *Asterina* it is found that the nature of its growth causes a spreading of the basal portion and results in a flattened fruit with the asci in a broadened hymenium. As a consequence of this spreading of the fructification in *Asterina*, in close contact with the surface of the host, the stromatic cover is also spread and its margin, instead of folding under as in *Meliola*, is extended and exposed at all times thus forming a clypeate stroma.

Varying degrees of hyponasty may be followed through the Microthyriaceae to the extreme case in *Trichothyrium* where, due to an excessive growth of this sort, the margins of the discus-shaped ascocarps are turned upward from the substratum when mature. Instead of removing the Microthyriaceae, as has been suggested, to a position within the Discomycetes it would seem more natural to retain them among the Perisporiales, or at least rank them as an offshoot from that order. Their flattened form and the fact that their perithecia (thyriothecia and katothecia of von Höhnel, 1910, 1917) develop under a radiate stroma does not seem sufficient justification for the change. It also appears that the reduction which has taken place in the perithecial wall results in a seeming parallelism with the Dothideales, and is probably due to similar factors.

A thin heavy-walled stroma substitutes for the outer protective wall of the perithecium in a number of instances.

The presence of spermatia would seem to indicate that possibly Arnaud (1910) is justified in the removal of *Limacinia*, *Capnodium* and other related genera formerly placed in the Perisporiales to the Amphisphaeriaceae among the Sphaeriales. Here again it seems more practical to me, however, to retain them within the Perisporiales as an early branch from a point near where that order has its origin from the Sphaeriales, and as relatives of genera near *Parodiopsis*. Such a conclusion would justify Von Höhnel's erection of the family Capnodiaceae for their reception. Cytological investigation is needed in connection with these forms in order to fix definitely their exact position. From present indications it seems more probable that the presence of spermatia among certain genera of the lower Perisporiales should be considered indications of where divergence took place rather than warrant for their removal from that order.

Arnaud (1918, 1925) considers that the Dothideales and the Microthyriales are orders which have had a parallel development. In this later arrangement of his he places *Meliola* at the top of the Dothideaceous branch as dissociated and superficial rhizomophic forms. The Wardineae, including *Asterina*, he locates as the culmination of the Microthyriales. As he places the genera *Meliola* and *Asterina* each at the top of separate phylogenetic lines we must conclude that he considers these lines as approaching one another rather than developing in the usual manner of diverging ascent.

This removal of the *Meliolae* to the Dothideales cannot be accepted either on the basis of stromatic development or perithecial formation. They must be excluded from the Dothideales in the first case because their thin flammeaceous stroma has the totally different mode of development found among members of the Perisporiaceae and their relatives. In the second instance they are excluded because of the well developed ostiolate perithecium with protruding periphyses formed *under* the protection of this stroma. As at present restricted the Dothideales develop a plurilocular fructification. Though it is perfectly possible for a reduced stroma, and a consequent simplification of the fruit, to occur within this order, the Phyllacoraceae, where such tendencies appear, do not seem to offer a reasonable point of contact for a genus with the characteristics of *Meliola*. Further cytological study among the Perisporiales including more species of *Meliola* and related genera is much needed.

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## Explanation of plates

All figures were drawn with the aid of the Abbe camera lucida. Figure 5 is drawn to a magnification scale of approximately ×640; all other figures to one of approximately ×1075.

### PLATE 16

Fig. 1. Ascocarp anlage, end view in relation to leaf surface.

Fig. 2. The same as figure 1 but in side view; of approximately the same age.

Fig. 3. Young ascocarp in median section. The oögone appears in the center with its large fusion nucleus. From its basal cell two filaments of the investing hyphae which go to make up the perithecial wall can be seen, one on either side. The spirally twisted antherid appears beneath the oögone, while over all the hood-shaped stroma forms a complete protection.

Fig. 4. The ascogone shows a length of several cells with a branch beginning to develop from the penultimate. A stomatopodium appears at the entrance to the stomatal cavity and the whole growth is closely applied to the host cells.

Fig. 5. The core is continuing development beneath the stroma which has developed somewhat in thickness. The ascogone is heavy staining and appears near the center, while surrounding it appear cells partly ascogenous hyphal and partly perithecial.

Fig. 6. The ascocarp is assuming its spherical form, and the cells of the perithecial wall are clearly distinguishable within the stroma. The ascogenous hyphae fill the center.

Fig. 7. Normal epidermal and palisade cells of the host.

Fig. 8. The fungous filaments are closely applied to the surface of the heavily cutinized epidermis. This cutinized layer has been eroded, and the content of the epidermal cells shows that some injury has been sustained though no haustoria are present.

### PLATE 17

Fig. 9. The young asci are seen to arise from the basal region of the ascocarp. A few scattered paraphyses are present and periphyses are developing in the upper portion of the cavity. The flattened perithecial cells can be distinguished from those forming the stromatic hood.

Fig. 10. Crozier formation is typical.

Fig. 11. A single crozier and two young asci with fusion nuclei.

Fig. 12. In each ascus four spores are cut out simultaneously, each contains two of the original eight nuclei.

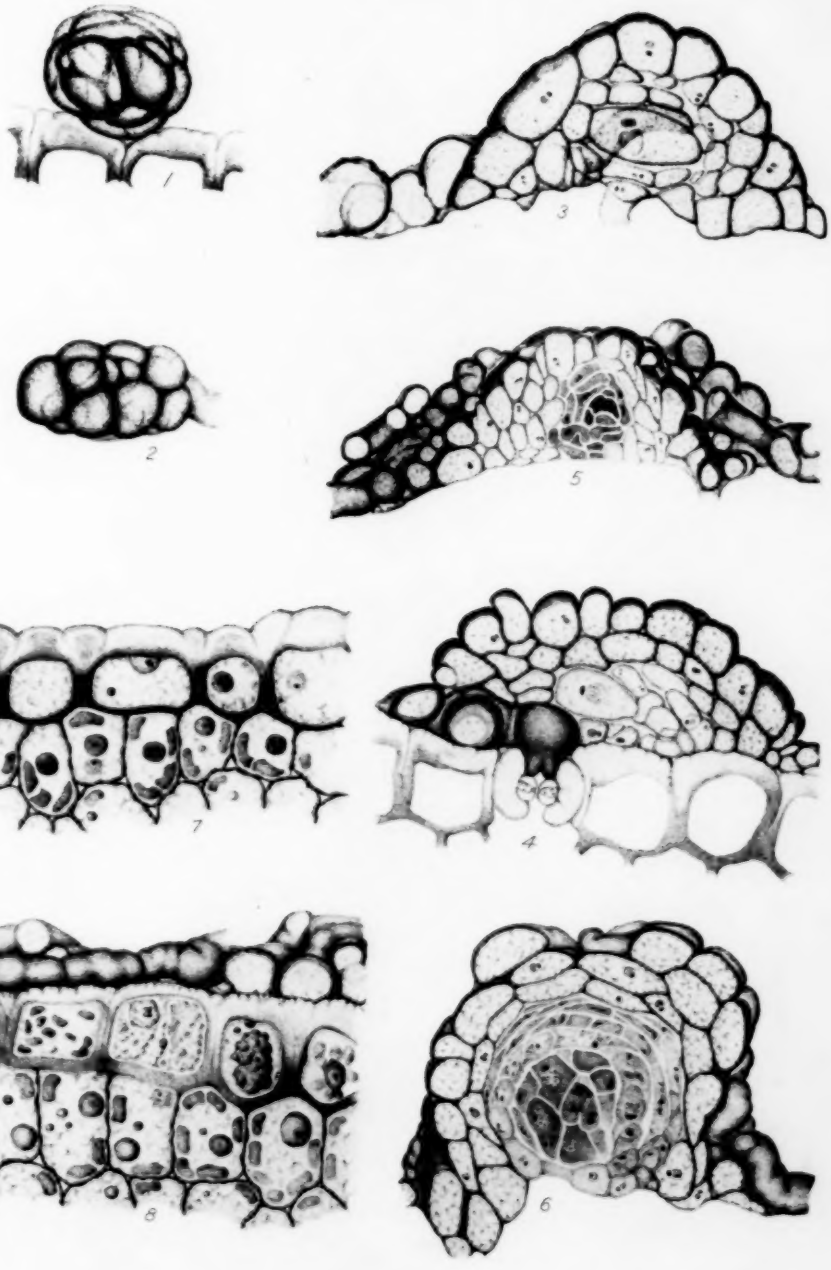
Fig. 13. As two of the spores develop the other two degenerate and finally disappear.

Fig. 14. The mature ascus contains normally two five-celled spores. Their middle cell contains two nuclei, while the others have but one each. These nuclei arrange themselves on the side of the spore away from its neighbor.

Fig. 15. In the development of the spore the two original nuclei divide to form four, and a daughter of each moves toward the ends of the spore and the terminal cells are cut off. The two nuclei remaining in the center then divide and one nucleus from each will be located in the center cell of the spore.

Fig. 16. When mature the spore is heavy-walled and the content is barely discernible.

Fig. 17. The periphyses push their way between the cells of the stroma and the ostiole is formed at the top of the ascocarp, but not till late and when mature spores are present.

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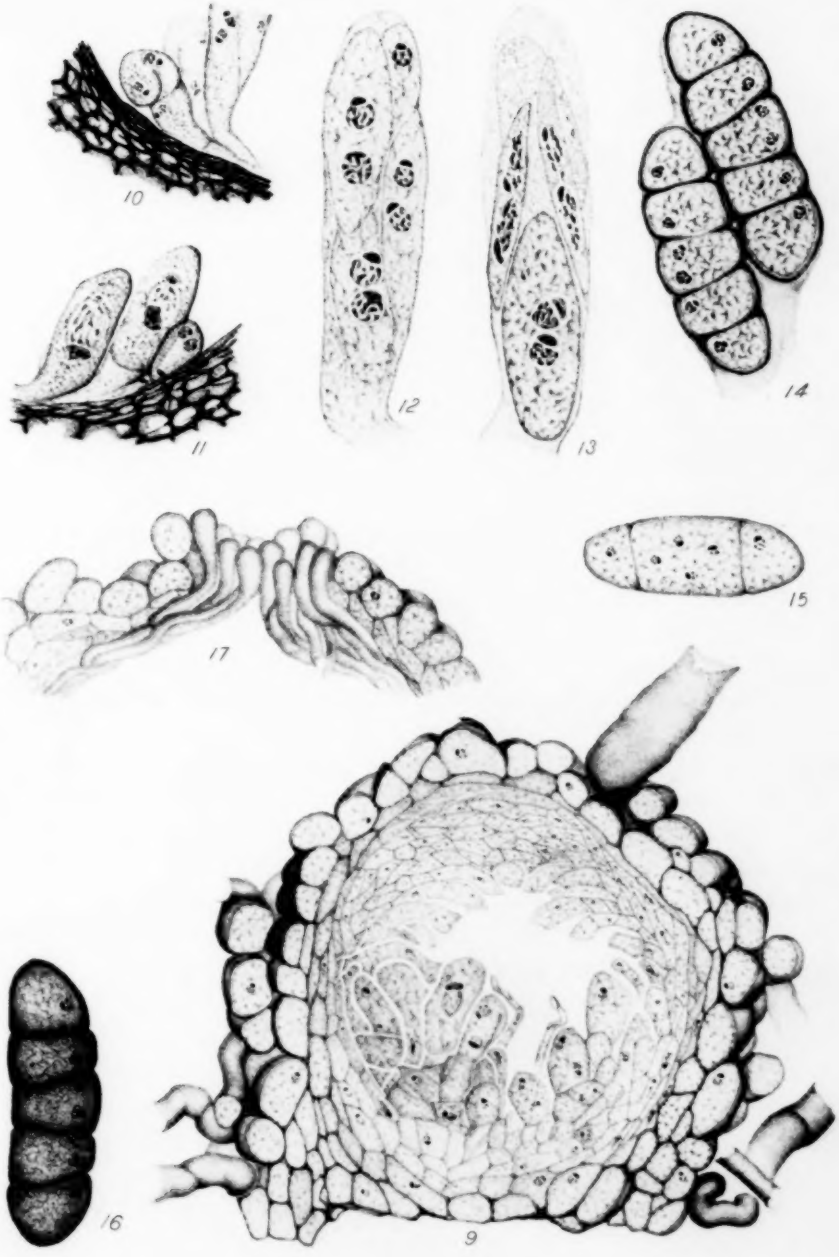


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# A progeny study of the so-called oak species Quercus Saulii, with notes on other probable hybrids found in or near the District of Columbia

H. A. ALLARD
(WITH FOUR FIGURES)

## FERTILIZATION PHENOMENA IN THE WHITE AND BLACK OAK GROUPS

Two distinct groups of oaks occur in the eastern United States, one known as the white oak group, the other known as the red or black oak group. So far as known all the American oaks of the white oak group mature their fruit the same year in which pollination takes place, making them annual fruited species. The species of the black oak group are dominantly biennial in the development of their fruit. Counting from the time of pollination all our Washington species belonging to this group require two years for the maturation of their fruit.

These contrasting behaviors probably rest upon fundamental physiological differences in the fertilization phenomena of the two groups at present not at all understood. When pollen reaches the stigma of members of the white oak group, the growth of the pollen tube containing the male cells follows an uninterrupted advance into the tissues of the style until the ovules are fertilized. In the case of the black oak group the typical biennial behavior occurs; the pollen falling upon the stigma begins its growth as in the white oaks, the pollen tubes invading the tissues of the styles until the stylopodium, which appears to be essentially the coherent basal portions of the three styles, is reached. For some unknown reason the pollen tube ceases further growth here during the current season of pollination, and appears to pass into a dormant or resting condition until the second spring, when fertilization of the ovules proceeds as in the annual fruited white oaks. In the case of the black oaks it would appear that the stylopodium is a sort of hibernaculum for the resting pollen tube. In some respects this is a most remarkable behavior and leads one to wonder if external environmental conditions may not modify this course of events, and perhaps allow the pollen tubes to make an uninterrupted advance into the ovules as in the case of the white oaks.

Several years ago while making studies of the effects of various lengths of day upon growth and reproduction in plants, the writer conceived the idea that perhaps a localized modification of the length of day upon the twigs and inflorescence of the willow oak *Quercus phellos* would disturb this distinctive cessation of growth and resulting dormancy of the pollen tube, and bring about an annual fruiting condition in the treated branches.

Accordingly, ventilated dark cases were so arranged on several trees at Arlington Farm, Virginia, that fruiting branches before anthesis could be subjected to ten hours of daylight only each day throughout the summer. These particular experiments were unsuccessful and the treated branches remained biennial in their fruiting behavior. Tests of a single season cannot be considered final, however, and it may be that experiments begun from the time of germination of the acorns, using various lengths of day would reveal an entirely different story for the initiation of the reproductive structures, and the subsequent annual or biennial behavior of the oaks. At the present time there is nothing to indicate why the pollen tubes of the black oaks should show the specific resting behavior in the stylopodium characteristic of their growth during the first season. The behavior still remains an enigma for future experimentation.

Natural pollinations are producing intra-specific hybrid forms now and then in the field, but so far as known, these hybrids in all instances are confined strictly to their own groups. It would seem that any white oak species in a locality can fertilize readily any other member of the white oak group. Likewise any black oak in a locality may, it would seem, quite as freely fertilize any other member of the black oak group.

These natural inclinations on the part of the oaks have given rise to quite an assemblage of intra-specific hybrids which have proven not only of much interest to botanists but a positive worry to systematists, bent upon an honest and helpful labeling of all plants in the field.

Even though in the case of the oaks wind pollination is the rule and the light wind-blown pollen is free to settle where it will, hybrid trees are always sporadic in their occurrence, and never common in any locality. In spite of the free intermingling of species everywhere, the purity of the various species is to be remarked upon rather than a positive, identifiable hybridity of the populations. As an offhand guess this would indicate, perhaps a self-prepotency for the oaks as has been found to exist in maize.

### ALBA × MONTANA

Several oak hybrids are already listed in our District Flora, of which little is definitely known concerning their parentage. Among these is the so-called species *Quercus Saulii* Schneid, supposedly representing the hybrid *Q. montana* Willd. × *alba* L.

In 1883 George Vasey,[1] a Washington botanist, described and illustrated several oak hybrids recognized in the vicinity of the District of Columbia. One of these was Saul's Hybrid (*Q. Saulii*). Vasey's illustration

[1] VASEY, GEORGE. On three hybrid oaks near Washington, D. C. Bull. Torrey Club **10**: 25–26. *pl. 28–30.* 1883.

of this oak shown in his plate 28 does not as well represent the leaf forms characteristic of individuals which I have found, as his plate 29, and perhaps plate 30. These two latter, however, he has considered to be hybrids of *Q. alba* with *Q. stellata*.

I have found several individuals of Saul's oak in the Washington region. A particularly fine large tree stands on Pershing Drive, near Maryland Avenue, Ashton Heights, Clarendon, Va. I have found other individuals near Chevy Chase Country Club. Almost at a glance one can detect evi-

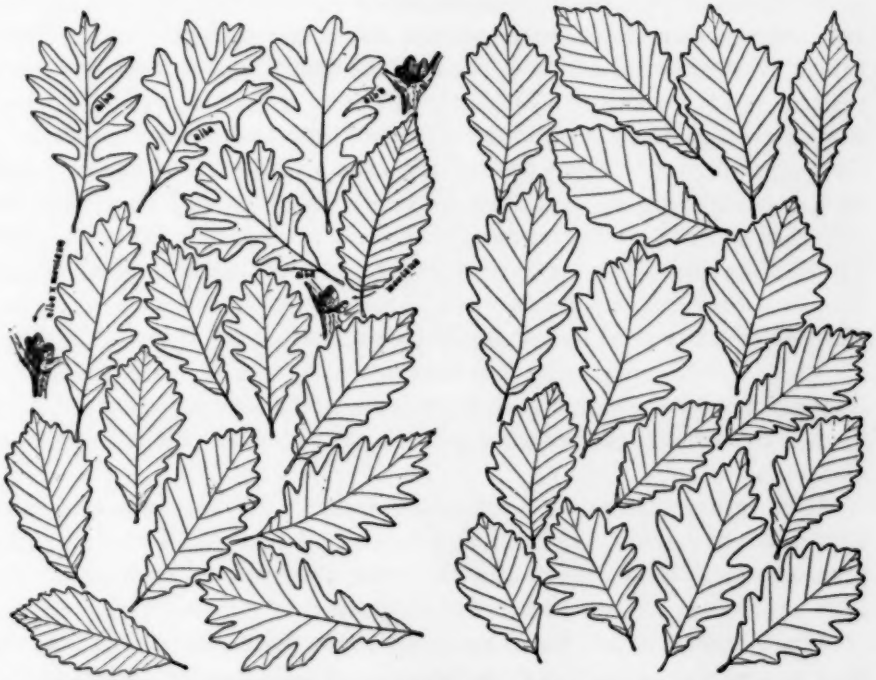

Fig. 1. Left. Leaves of *alba*, *montana* and leaves of the hybrid form *Saulii*, together with buds. *Montana* buds are shown near the petiole of the *montana* leaf. Right. Other leaves of the hybrid form *Q. Saulii*.

dences of *montana* blood in these forms, not only in the deeper even lobing of the leaves, but in the droop or hang of the foliage and in the size and shape of the acorns and the cup.

About ten years ago, I secured a quantity of acorns from the tree on Pershing Drive, and planted them in garden soil. About forty seedlings were obtained, the majority of which have been allowed to grow until the present time. Many of the individuals of this progeny have shown rapid yearly growth and the largest have now attained a height of 15 feet. A careful analysis of the progeny was made and a typical representative leaf

selected for illustration from each tree. At a glance it is seen that many intermediate forms have appeared, representing different degrees of approach to one or the other parent *montana* or *alba*. As a whole the progeny shows a dominance of *montana* characters, in the shallow, more numerous and uniform lobes of the leaves and the presence of more or less minute whitish pubescence beneath. However, there are individuals with larger and irregular lobing of the leaves, showing unmistakable white oak parentage.

With respect to the autumnal behavior of the individuals of this progeny, some striking features are shown. A number of trees show the more typical red-brown coloration of the *montana* parent; others show the more coppery red indicative of *alba* blood. Others have shown an almost entire dominance of yellow hues, giving evidence of little anthocyan in the leaves. One vigorous individual of particularly obvious *alba* stamp has assumed each year a most gorgeous, deep red coloration, such as I have rarely if ever seen equaled by any member of the white oak group. This particular tree likewise loses all its leaves promptly, behaving less like a typical white oak, and more like the chestnut oak in this respect. Another vigorous individual with a decided hybrid stamp approximating more closely the *montana* type of leaf, except that it is narrower and more elongate, assumes a deep red brown coloration each autumn, but the leaves show a decided tendency to cling to the branches as is the characteristic behavior of many *alba* trees.

With respect to autumnal coloration, leaf fall, etc. it is indicated that we are dealing with individual and hereditary features, which in their genetic behavior may show unit-character relationships such as obtain with leaf-form or any other feature of vegetative or reproductive expression.

When natural hybrid forms are found in the field, it is evident that we have no assurance as to what generation is actually involved, whether the original cross appeared in the $F_1$ generation or some subsequent generation descending from this. In the case of all fruit which I have obtained from *montana* × *alba* (*Saulii*) trees, the acorn and cup have been decidedly of the *montana* type.

To say the least, it is evident that the so-called oak species *Quercus Saulii* combines *montana* and *alba* blood. With greater numbers representing the progeny, it is possible that far greater extremes of variability may yet be found, with much closer approximations to the *alba* parent.

### ABERRANT FORMS WHICH APPEAR TO REPRESENT HYBRIDS

*Phellos* × *marilandica*. A small tree found at Lyon Park in a colony of *Q. phellos*, *Q. marilandica* and other upland oaks. The leaves are very vari-

able in shape ranging from the unlobed type through forms slightly wavy-margined to more extreme forms. In some instances, one weak obtuse or rounded lateral lobe is present; in others a pair of lateral lobes of this type occurs. The more prominent lobes occur well toward the apex of the leaf. These as well as the apex of the leaf are conspicuously bristle-pointed. The leaves are thick and rather coarse in texture, with a somewhat wavy surface, and average around 4 to 4.5 inches long and 1.25 to 2 inches in width. The petiole is very short—only 1/8 to 3/16 inches in length. The undersurface is mostly smooth except for a whitish scattered pubescence along the midrib and in the vein axils. The color of the leaves is a rather deep green, deeper than that of *phellos*.

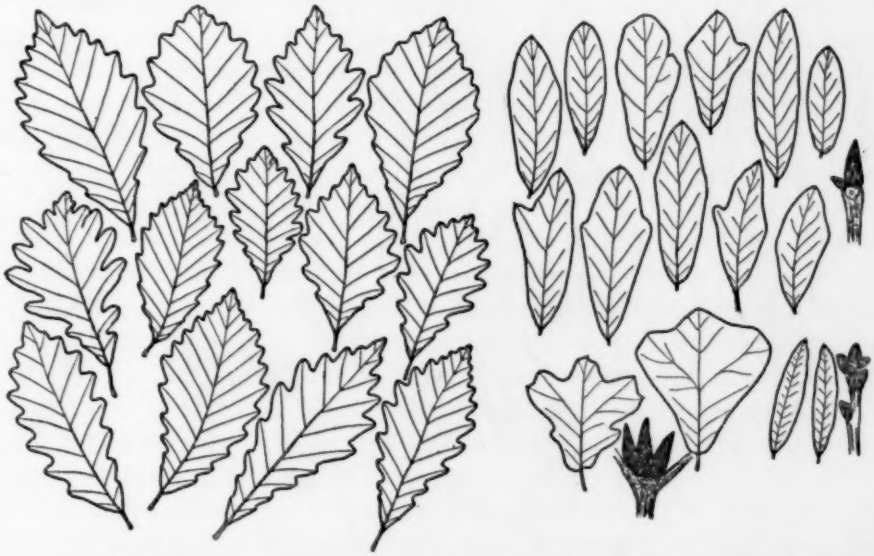

Fig. 2. Left. Additional leaves of the hybrid form *Q. Saulii*. Right. Top and middle row showing leaves and buds of supposedly hybrid form *phellox*×*marilandica*. Lowermost row, two leaves and buds of *marilandica* at left; two leaves and buds of *phellos* at right.

The buds are much more elongated and sharp pointed than in the case of the willow oak. This feature together with more pronounced pubescence of the bud scales and the more pubescent condition of the new twigs, affiliates the tree more closely with *marilandica*.

The very short stout petioles of the supposedly hybrid forms would suggest *marilandica* blood rather than *rubra* (*falcata*).

It is interesting to note in this connection that N. L. Britton[2] in 1882 was the first to describe a *phellos*×*marilandica* cross as he judged certain

[2] Britton, N. L. On a hybrid oak near Keyport, N. J. Bull. Torrey Club 9: 13–15. *pl. 10–12*. 1882.

oak trees to be occurring near Keyport, New Jersey, giving it the specific designation *Quercus Rudkini*. Britton illustrated his paper with several color plates of leaves of his supposed hybrid. In form these very closely resemble the leaves of my own tree. C. S. Sargent[3] in 1895 illustrated the supposed cross of *phellos*×*marilandica*, which, like Britton's illustrations, agree closely with my own material.

In 1907, D. T. MacDougal[4] made progeny studies of this oak named *Q. Rudkini*, securing about 100 seedlings from planted acorns. While he found much variability in the progeny he concluded that this was not

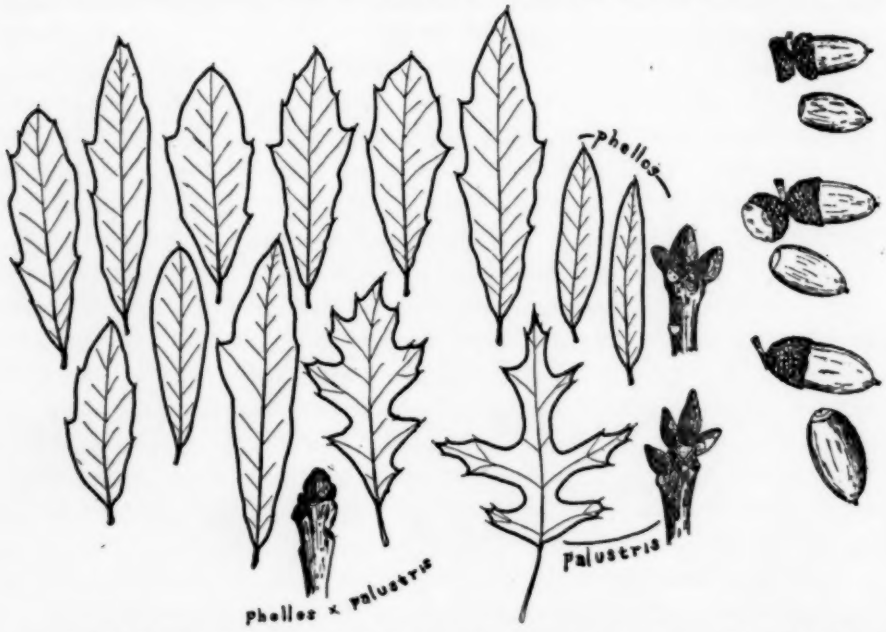


Fig. 3. Left and center. Leaves and buds of the supposedly hybrid form *palustris*×*phellos* and of the parent forms *phellos* and *palustris*. Right (above) Acorns of *alba;* (middle) *Saulii;* (below) *montana*.

more extreme than actually occurs in good oak species with a unified heredity. His final conclusion was that there was little in his progeny analysis to indicate actual hybridization, and that *Q. Rudkini* must be regarded as a good species until further studies disproved its taxonomic standing.

In this connection it may be said that the oaks found by Britton could still have a hybrid origin, and yet show a reasonable degree of variation in

[3] SARGENT, C. S. The silva of North America. **8**: *pl. 437*. 1895.

[4] MACDOUGAL, D. T. Hybridization of wild plants. Bot. Gaz. **43**: 45–58. *f. 1–4*. 1907.

the progeny as indicated by MacDougal. If a hybrid form appears, no one knows what generation is involved, and the trees in question may have been many generations removed from the original cross. A thousand trees would probably show greater extremes of variation than one hundred trees if a cross were involved.

*Phellos*×*palustris*. Young trees supposedly representing this cross have been planted on Pershing Drive continued, just east of Glebe Road. A considerable number of willow oak trees have been planted in this subdivision, two of which show leafage suggesting hybrid parentage. The oblong-lanceolate leaves are very variable in shape, ranging from forms with entire margins to those with rather shallow lobes or mere bristle-pointed teeth. Their average length is 4 to 4½ inches by 1 to 1½ inches wide. The petiole is very short and rather stout, averaging ⅜ inch long or less. The glabrous leaf-blade is bright green in color; in autumn the midrib and petiole assuming a deep crimson shade, which may even extend to the leaf blade. It is obvious that these oaks do not represent either the *phellos* type or the *palustris* type. The presence of teeth and lobes, the autumnal coloration and the general shape of the tree suggests *palustris* parentage. The very short petioles, however, are quite unlike the slender, flexible petioles of *palustris*, which are usually 1¼ inches in length.

*Imbricaria*×*marilandica*. In 1930 several young trees were found in the woods near the head of Pimmit Run which give indications of being hybrid forms. In the immediate locality trees of *imbricaria* and *marilandica* were growing, and in so far as circumstantial evidence can reveal the truth on the basis of parental resemblances, it would appear that these two species have been involved in the supposed cross.

In general shape the leaves are oblong-lanceolate, 7 to 9 inches long, and 1½ to 3½ inches in width. The petiole is about ¾ to 1 inch long and rather slender. There is great variability of leaf-form on the same tree, the leaves varying from entire to slightly sinuate lobed, or with a pair of bristle-pointed lobes near the apex. The undersurface of the leaves is uniformly fine whitish puberulent. The buds are more elongate and acute than in the case of *imbricaria*, but like this species nearly smooth as are the twigs below. The autumnal coloration assumed by the leaves in some instances was a most gorgeous deep crimson. While it is possible *rubra* (*falcata*) parentage could be involved, the general appearance of the leaves and the deep red coloration indicate *marilandica* affiliations rather than *rubra* (*falcata*).

In 1877 George Engelmann[5] reported finding a tree near St. Louis in

[5] ENGELMANN, G. About the oaks of the United States. Trans. St. Louis Acad. Sci. 3: 372–400; 539–543. 1868–1877.

1849 which he regarded as a cross between *imbricaria* and *marilandica*. The leaves appeared to be those of the former with a hint of the peculiar lobing of *marilandica*, being coarsely 3-dentate at the apex, or with a few teeth on the sides. In some instances the leaves were entire.

C. S. Sargent[6] in 1895 illustrated material supposedly derived from this cross *imbricaria*×*marilandica*, which bears a striking resemblance to my own material.

Bartram's Oak, *Q. heterophylla* Michaux (*phellos* L.×*maxima* (Marsh.) Ashe). This is an uncommon form in the District Flora, although I have been fortunate enough to find material of this botanically historic species. No oak in our American flora has acquired the romance of botanical interest that this oak has inspired since the younger Michaux described it as a new species in 1810. A long line of the foremost botanists of America as well as many others of less distinguished note have ventured their opinions considering the origin and affiliations of this historic form. Some have vouched for its hybrid origin; others have as dogmatically affirmed against such a possibility.

L. S. Gale,[7] writing in 1855, was most strenuously opposed to such an origin, and even went so far as to deny all hybridization among oak species. It may be stated here, however, in due respect to the rather decided opinions of Gale that he appears to have made some of the first sincere efforts to unravel experimentally the heredity of the Bartram Oak. Gray in 1848 considered it a possible cross between *phellos* and *falcata*. From 1851 to 1855 Gale planted acorns of the Bartram Oak which he discovered in Washington. Seedlings which he secured resembled the parental form closely. At the same time he attempted to hybridize by careful control methods of bagging with cloth balloons, as he called them, *falcata* with *phellos* and the Bartram form. As a result of his first pollination experiments in 1852, acorns were obtained from *phellos* pollinated with *falcata*, and *falcata* pollinated with *phellos* pollen. It is evident that Gale was even expecting a direct effect of the pollen upon his crossed acorns, for he remarked that the acorns always resembled the mother parent. When the planted acorns gave rise to seedlings there appeared to be no observable difference between the seedlings arising from the bagged acorns and those unbagged from the same trees. It is here that Gale was wrong, for the Mendelian behaviors of crosses had not at that time enlightened the botanical world. Today we know that the $F_1$ plants may have been strikingly like one of the parents, and that the breaking up of a dominant or a

[6] SARGENT, C. S. Op. cit., Plate 433. (See footnote 3.)

[7] GALE, L. D. On the oaks of the District of Columbia. Proc. of the Nat. Inst. Washington, 1: 67–77. *f. 1, 2.* 1856.

blended $F_1$ uniformity would become evident in later generations. In the spring of 1854 Gale carried out similar pollination experiments, using more closely woven bags, and secured no acorns whatever.

It would appear that the Bartram form described by Gale was the second positive discovery of a Bartram Oak. About the year 1855, trees of a similar type were found at Mt. Holly, New Jersey, and subsequently at various other stations in New Jersey, Delaware and Staten Island, New York, and the range of the form has now gradually extended well into the South. Opinions of botanists that had centered of necessity around the

Fig. 4. Leaves and buds of the supposedly hybrid form *imbricaria*×*marilandica*. At extreme right a leaf and buds of *imbricaria* are shown. Buds below and two adjacent leaves at left represent *marilandica*. Remaining illustrations represent the suspected hybrid.

single original specimen of Michaux, until about 1850, were now directed to a group of sporadic occurrence. At one time or another, nearly every deep-lobed member of the black oak group has been considered one of the parents in a *phellos* combination, including *rubra* (*falcata*), *coccinea*, *palustris* and *velutina*. Strangely enough, *maxima* (Marsh.) Ashe, had never been mentioned.

In 1888, as a result of his studies of forms resembling the Bartram Oak found at Tottenville, Staten Island, New York, Arthur Hollick[8] finally

[8] Hollick, Arthur. A recent discovery of hybrid oaks on Staten Island. Bull. Torrey Club **15**: 303–309. *pl. 83–85.*

concluded that this oak is the result of the cross *phellos*×*rubra* (*maxima*) as the northern red oak is now designated. This original opinion is of some interest, in the light of a careful progeny analysis made by D. T. McDougal[9] in 1907. A progeny of 55 seedlings obtained from acorns of a Bartram form gave a range of variation extending from *phellos* to *maxima*. As a result of his analysis, MacDougal concluded that Bartram's oak is an indubitable hybrid which has arisen between *phellos* and *maxima*.

This would seem to establish fairly accurately the status of the puzzling Bartram Oak, and withdraw it from the *phellos*×*velutina* parentage which has been ascribed to it in the "Flora of the District of Columbia and Vicinity," Contr. U. S. Nat. Herb., Vol. 21, 1–329. 1919.

*Imbricaria*×*velutina* (*Q. leana* Nuttall) is an uncommon form in the District of Columbia.

*Alba*×*stellata* has also been reported in the *District Flora*, and has been variously figured.

It is evident that the District of Columbia embracing an area of no large size offers rather interesting opportunities for the study of hybrid oak forms. As a matter of fact this limited area is especially rich in oaks, 14 undoubted species being listed in the *District Flora*, one, *ilicifolia*, of less certain occurrence, together with four presumably hybrid forms.

In this connection it is interesting to note that at the time Gale was writing in 1855, *Q. imbricaria* was not considered indigenous to the District, and even *Q. rubra* (*maxima*) and *Q. bicolor* were considered extremely rare. As a matter of fact Gale reported that he added *rubra* for the first time to the District flora, which had not been reported in the Flora Columbiana of John A. Brereton, published in 1830. Gale found a single tree on the banks of Rock Creek in a cool shaded ravine, and thought this was the sole representative of a northern species. He was the first to record Bartram's oak in the District of Columbia on his own statement. In 1855 the chestnut oaks *prinoides*, *prinus*, and *Muhlenbergii* appear not to have been reported in the District assemblage of oak species.

It would seem that nature is producing rather rarely and sporadically hybrid forms. This suggests that a most attractive problem awaits some young, hopeful school of field botanists interested in further studies of of natural hybrid forms, as well as in the experimental production of new hybrids. A study of such hybrid progenies beside the parental seedlings would quickly reveal to what degree hybrid vigor may obtain, and settle many little nomenclatorial troubles in the *Quercus* assemblage.

In every locality there is an urgent need for a careful recording of all

[9] MACDOUGAL, D. T. Op. cit. (See footnote 4.)

hybrid or anomalous forms in order that they may be preserved whenever possible, or at least kept from utter extinction in their progenies. These rare and sporadic incidents of nature are too interesting and beautiful to treat with indifference, with a flora being woefully mistreated and reduced to pitiful remnants in many sections. It would be well if parks or arboretums could be maintained in the Washington region where anomalous or hybrid forms could find a home for future botanical studies.

In spite of the sporadic occurrence of hybrid forms let no one think it is an easy matter to give readily every oak tree to be met with an indisputable specific label, for many categories of variation more or less local or regional obtain for every species in the field. In the past, unfortunately, the tendency has been shown to give specific names rather freely to every unusual form or supposed hybrid encountered in the field. In more than one instance the result has been to clutter the nomenclature of the oaks with many species names which really have no good standing as representing distinct species composing the facies of the flora of a region. Surely the species concept must carry with it some attention to the progeny constancy of a form, either as determined by the general resemblances of a natural assemblage in the field, or by actual progeny studies. Many of our listed hybrid species would unquestionably show a most bewildering array of intermediate forms and perchance parental reversions if their progenies were intensively analyzed, as in the case of the Bartram Oak. If it is legitimate taxonomic spirit to name in turn these varied assortments representing all manner of combinations of leaf and fruit characters which are certain to occur in hybrid progenies, a world of intergrading oak species is yet to be listed by zealous students of oak hybrids. Such a viewpoint, however, could only result in hopless confusion for the naturalist.

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# Useful plants of Yucatan

ROLAND M. HARPER

Most of Mexico is rather mountainous, with great variations in rocks and minerals, soil, climate and vegetation in comparatively short distances. But the peninsula of Yucatan, comprising the states of Campeche and Yucatan and the territory of Quintana Roo, with a combined area of about 55,000 square miles, differs markedly from the rest of the country in being a plain of horizontally bedded late Tertiary limestones, broken by a few low ridges, and rising gradually to an elevation of some 900 feet at a distance of 100 miles from the coast. There are practically no surface streams, the water circulating in subterranean channels in the limestone, with many natural well-like openings of various sizes, known as *cenotes*, affording an unfailing water supply for the former and present inhabitants. Being within the tropics, the climate is always warm. The northern coast is rather dry, but farther south the rainfall is ample, and most of it comes in summer, as in southern Florida, which resembles Yucatan also in many of its features of geology, topography and vegetation. (And indeed Key West, Florida, is nearer to the northeastern corner of Yucatan than it is to Jacksonville.)[1]

Yucatan is noted among archaeologists the world over for having been the home of the Mayas, whose temples and inscriptions, hewn from the native limestone, show them to have had the highest civilization in the western hemisphere about a thousand years ago. This civilization had already begun to decline before the Spanish invaders arrived, however, for reasons not fully understood, and the Maya Indians who inhabit the wilder parts of the peninsula today are little better than savages.

The fish and game resources of Yucatan must have been inferior to those available to the North American aborigines, and the Mayas, who had little commerce with other peoples, must have lived mainly on vege-

[1] There is a vast amount of literature on Yucatan, largely archaeological. Besides the volume on which the present paper is based, and other botanical literature referred to in it, the following reasonably accessible works will give a pretty good idea of the natural conditions there.

Leon. J. Cole. The caverns and people of northern Yucatan. Bull. Am. Geog. Soc. **42**: 321–336. *f. 1–14.* May, 1910.

Ellsworth Huntington. The peninsula of Yucatan. Bull. Am. Geog. Soc. **44**: 801–822. *f. 1–11.* Nov. 1912.

See also H. H. Bartlett, A biological survey of the Maya area. Bull. Torrey Club **59**: 7–20. 1932.

table products. During the centuries that they lived there, they must have found uses for a large proportion of the native plants; and their plant lore has been passed on pretty well to the present inhabitants, both aboriginal and Caucasian. They had a few important cultivated plants which originated in America even if they were not indigenous to Yucatan, such as cotton, corn, beans, and sweet potatoes.

In modern times the exports from Yucatan have been almost entirely vegetable products, for the only mineral resource, limestone, is common in most other countries, animal products are unimportant, and there are no manufactures to speak of. Exports of logwood and mahogany from the peninsula are said to have begun two centuries ago or more. The most important forest product at present is chicle gum, but that is surpassed in value by henequen fiber (also known as sisal), derived from cultivated plants of American origin.

Existing knowledge of the plants of the peninsula has been brought together in convenient form in Paul C. Standley's recent Flora of Yucatan.[2] It happens that the author had never been in Yucatan, but he had been in other parts of Mexico, and in Central America, and a few years ago he published a voluminous work on the Trees and Shrubs of Mexico.[3] In the Yucatan flora all the plants, both wild and cultivated, about 1250 species, known to occur in the peninsula, are listed, with copious notes on Maya and Spanish names, uses, etc. The chief source of information was the work of Dr. George F. Gaumer, a physician and amateur botanist, who lived in Yucatan from 1885 to his death in 1929. Another important contributor was Dr. Charles F. Millspaugh, who was also a physician before he was a botanist. He visited the peninsula and neighboring islands in 1894 and 1899, and spent much time during the remainder of his life in studying at the Field Museum the collections made by himself, Gaumer and others. Several other botanists who either visited Yucatan or described plants from there are mentioned in the bibliography, which covers nearly ten pages of Standley's work. Even yet, according to Mr. Standley, the flora is imperfectly known, especially that of the southern part of the peninsula, which is difficult to explore on account of the dense forests, the savage inhabitants, and the danger of malaria and other tropical diseases.

But enough is already known to show that the area contains a remarkable number of useful plants, especially medicinal ones. The information about medicinal plants may be more complete than usual, on ac-

[2] Field Museum, Bot. Series, **3**: 155–492. (Publication 279.) Sept. 1930. Reviewed in Tropical Woods (New Haven) **24**: 31–35. Dec. 1930.

[3] Contr. U. S. Nat. Herb., vol. 23. 5 parts, 1721 pp. 1920–1926.

count of the medical interests of Drs. Gaumer and Millspaugh, but such plants seem to be rather partial to limestone regions anyway.[4]

Standley's Flora of Yucatan will of course be frequently consulted by persons interested in tropical American plants, but those who merely look up the references to various species will not get the whole story. On account of the large number of economic plants mentioned in it, and the full notes on them, it has seemed worth while to the writer (who has never been any nearer to Yucatan than Key West) to pick out such plants from the text and group them by uses; which was a rather tedious task, but makes an interesting story. It would take too much space to mention them individually, and the names of most of them might be unfamiliar to most readers of the Bulletin; but that might be done for local consumption at some future time when the region is more thickly settled and the flora better known. For the present the approximate number of species in each large economic group will be indicated, and some of special interest mentioned, while in the smaller groups most or all of the species may be referred to. Cultivated plants of Old World origin enumerated by Standley will not be considered here, however, for those could be grown in any other region of similar climate just as well.

In Yucatan, as in most other tropical countries, woody plants constitute the bulk of the vegetation, and they are also more numerous in species than they are in cooler climates. Of all the native plants listed by Standley, 172 may be classed as trees, 226 shrubs, 71 woody vines, and 467 herbs; though of course there are many intermediate forms, and no two

[4] See Torreya **30**: 75. June 1930.

Since this manuscript was sent to the editor—and therefore too late to be thoroughly digested now—the Department of Middle American Research of Tulane University has published a 359-page bulletin or volume entitled *The ethno-botany of the Maya*, by Ralph L. Roys. (Middle American Research Series, Publication no. 2. August, 1931.) It was nearly all written before the publication of Standley's Flora of Yucatan, but the author corresponded with Standley, and utilized some of his material in manuscript form.

A catalogue of symptoms, with the plants prescribed for them, and copious quotations and translations from Maya texts, occupies over 200 pages, and an annotated alphabetical list of Maya plant names, with their scientific equivalents and therapeutic uses, over 100 pages. (A similar but more condensed list of animals occupies 17 pages.) An index of botanical names includes over 600 entries, exclusive of synonyms, but no page numbers. However, the Maya equivalents are given, and can be looked up in the alphabetical list.

Little is said about plants used for other purposes than medicine, except in a six-page chapter on the climate and food supply of Yucatan, near the end. A bibliography, with many of the citations incomplete as to page numbers, and including much relatively inaccessible manuscript material, occupies the last eight pages.

persons would count them in the same way. The useful plants are distributed in about the same proportions.

### SHADE TREES AND ORNAMENTALS

The only native plants specially noted as used for shade trees are *Achras Zapota* (which is useful in several other ways, as noted farther on), and *Gliricidia sepium*, a small leguminous tree called *zacyab* by the Mayas and *madre de cacao* by the Spaniards. The latter name refers to its use for shade in cacao plantations in Mexico and Central America, just as some other trees are used to shade coffee.

Many plants are mentioned as being handsome when in bloom, but the number of natives cultivated for ornament apparently does not exceed a dozen, if Mr. Standley's information was reasonably complete. Among these are *Mirabilis Jalapa* and *Dahlia variabilis*, familiar in American gardens, which are believed to have originated somewhere in Mexico, but not in Yucatan.

Two small trees, *Jatropha Curcas* (Euphorbiaceae) and *Spondias purpurea* (Anacardiaceae) are said to be often planted for living fence-posts. Two large shrubs, *Urera baccifera* (Urticaceae) and *Pedilanthus itzaeus* (Euphorbiaceae), are used for hedges, and some of the cacti may be used in a similar way, as they are elsewhere in Mexico.

### TIMBER TREES

In the first two parts of Standley's Trees and Shrubs of Mexico 26 species of *Pinus* and 112 of *Quercus* are listed, and the supplement in the last part adds 145 more of *Quercus*.[5] But neither pines nor oaks are definitely known in Yucatan, though Standley mentions rumors of a pine on ridges in the extreme south, which is probably *P. Caribaea*, the same species that is characteristic of southern Florida, western Cuba, and British Honduras. And if that region were better known some species of *Quercus* night be found there too, as there are a few in Cuba and Central America. However, even without pines and oaks, Yucatan does not lack timber. About twenty species of trees are reported by Standley as used in the construction of buildings, and about one-third of these belong to the families formerly included in Leguminosae, which are largely represented in tropical forests all around the world. One or two others are used for

[5] Nearly all these supposed additional species of *Quercus* were described by Trelease in 1924. Apparently *Quercus* in Mexico has been having a "boom," like that of *Crataegus* in the United States a generation ago. (See Geol. Surv. Ala., Monog. 9: 203–208. 1928.)

posts and poles, and about a dozen trees that are too small or rare or hard for ordinary lumber are used for cabinet-making and similar purposes. Mahogany, one of the best of all cabinet woods, was formerly an important export.

## FIBER PLANTS

Several tough woody vines, belonging to the genera *Paullinia* (Sapindaceae), *Arrabidea*, *Cydista* and *Pithecoctenium* (the last three Bignoniaceae) are used like ropes for binding the poles of roofs, walls or fences together, and coarse ropes and twine are made from the bark of such small trees and shrubs as *Bauhinia*, *Abutilon*, *Hibiscus*, *Hampea*, and *Guazuma*, most of these belonging to the Malvaceae and allied families.

Baskets, mats, thatched roofs, or brooms are made from *Typha angustifolia*, two sedges, two palms, and two shrubs of the genus *Acalypha*, which is represented in the eastern United States by a few weeds.

A malvaceous weed, *Sida acuta* (common also in Florida, where there are a few related species with similar properties), yields a strong bast fiber formerly used for making hammocks. Sea-island cotton, of the same family, was cultivated by the Mayas in pre-Columbian times, and has been exported, especially during our Civil War, but is now grown only for home consumption. *Ananas Magdalenae*, a near relative of the pineapple, is an important fiber plant, not certainly known in the Yucatan peninsula, but believed to occur in the southern part, as it does in Guatemala, not far away.

The most important export from Yucatan at the present time is henequen or sisal, a fiber from the leaves of two or three species of *Agave*, whose classification is still a little uncertain. Standley lists 170 species of *Agave* in the first part of his *Trees and Shrubs of Mexico* (though they are not what one would ordinarily call trees or shrubs), and 17 more in the supplement. Some of them are ornamental, some yield beverages, and some fibers; and some have been cultivated so long that they have developed varieties that cannot be assigned to any native home. Henequen was known and used by the ancient Mayas (who had several different names for it), and had already been transplanted to the Old World before the botanists classified it; and some of the species were originally described from plants cultivated in Europe, which complicates matters still further. From this fiber is made nearly all the binder twine used by the wheat growers of the United States and other countries. It is now grown in vast plantations in the drier and more accessible northern parts of Yucatan, and it brought considerable wealth to the state about the time of the World War; but since then the competition of Java and East Africa has

hurt the business.[6] The fibers of different species of *Agave* differ in quality, and there are differences of opinion as to which is the best; the British preferring that raised in their colonies.

Short fibers from the heads of cat-tails, from the trunks of the thatch-palm (apparently the same species as on the Florida Keys), and from the seeds of *Clematis dioica* and two species of *Ceiba* (Bombacaceae) are used for stuffing pillows, cushions, etc.

### DECORATIONS

The red and black seeds of two leguminous vines, *Abrus precatorius* and *Rhynchosia pyramidalis*, are used for necklaces. The corollas of two species of *Jacquinia* (Theophrastaceae) and of *Plumeria alba* (Apocynaceae) are strung on cords for decorations for festal occasions.

### FORAGE PLANTS

The principal wild forage plants are five or six coarse grasses (quite unlike the lawn and pasture grasses of temperate regions), *Viguiera helianthoides*, a coarse herb of the Compositae, the leaves and twigs of *Brosimum Alicastrum* (breadnut or wild cherry, of the Moraceae) and *Aeschynomene fascicularis* (a leguminous shrub), and the pods of *Prosopis Chilensis*, which is congeneric with the mesquite of Texas and adjoining states.

### HUMAN FOODS

Plants used for human food are so numerous that they may well be subdivided according to the parts used. There are two important root crops, the cassava and sweet potato, which are certainly American, but have been cultivated so long that their exact origin is unknown. Of the former (genus *Manihot*, family Euphorbiaceae) Standley lists four species from Yucatan. The first two are wild plants of no importance, though one of them, *M. Carthaginensis*, or what passes for it, is a small tree now cultivated in Florida for ornament or as an oddity. *M. dulcis*, the sweet cassava, said to be non-poisonous, is used both as a vegetable and as a source of starch. *M. esculenta*, which is poisonous until cooked, but widely used in tropical America, is said to be native of Brazil, but is believed to have been brought to Mexico before the Spanish conquest.

Other "vegetables" are the young inflorescences of *Chamaedorea gram-*

[6] The population of the state of Yucatan increased 5.8% between 1910 and 1921, while the rest of Mexico lost population; but the increase between 1921 and 1930 was only 7.3%, as compared with 14.4% in the whole country. Its capital city, Merida, ranks about fifth among the cities of Mexico in number of inhabitants, and is said to be very modern in appearance.

*inifolia*, a small palm, the young leaves of *Jatropha aconitifolia*, a small tree of the Euphorbiaceae, and the young fruits and ripe seeds of *Ceiba aesculifolia*, which is one of the large trees.

Wild edible fruits, either eaten raw or made into preserves, or both, come from about 12 large trees, 20 small trees, 2 woody vines, 5 shrubs and 6 herbs, which it would take too much space to list separately.

The most important seed eaten is *Zea Mays*, Indian corn, which has been cultivated so long that its origin is unknown, and it is no longer found wild anywhere. The Mayas had many different names for forms and parts of the plant and products derived from it. Standley says: "Upon the maize plant is based the whole Maya civilization. Exhaustion of the soil consequent upon the growing of the plant is believed to have caused the successive migrations."[7]

Two or three species of beans were known to the Mayas, and the same ones are now commonly cultivated in the United States; but, as in the case of the corn, their origin is unknown.

The cocoanut is common along the coast, as in all tropical countries, but it is believed to have been introduced by the Spaniards, as there is no Maya word for it.[8] Four or five other wild trees yield seeds that are eaten.

Beverages are made from the bark of *Lonchocarpus longistylus*, a leguminous tree, and from the seeds of one or two species of *Theobroma*, the cacao or chocolate tree.

Honey comes from the flowers of three trees, three shrubs and two herbs specially mentioned by Standley, and doubtless from many other species.

Flavoring materials and condiments are obtained from *Vanilla fragrans* (native in tropical America, but now cultivated mostly in the Old World), *Piper auritum* and perhaps others of that genus, *Pimenta officinalis* (allspice, of the Myrtaceae), *Capsicum annuum*, and a few other native plants.

## MEDICINAL AND POISONOUS PLANTS

Among medicinal plants there are all gradations between important ones that have obtained world-wide recognition, and those whose virtues

[7] Although corn is believed to have originated in Mexico or some other warm country, most of the American crop is now grown in the northern half of the United States. It is seldom seen in southern Florida, but that may be partly because it is attacked there by pests that were unknown in the time of the Mayas, and partly because present economic conditions make it more profitable for that part of Florida to raise tropical and semi-tropical fruits and early vegetables, which bring a much higher return per acre.

[8] For a recent and easily accessible account of the history of the cocoanut see J. K. Small, Jour. N. Y. Bot. Gard. **30**: 153–161, 194–203. 1929.

are doubtful or imaginary. Every civilized country has its own pharmacopoeia, which naturally gives preference to its own products, especially when a local and a foreign drug have similar properties. A drug map of the world by Dr. E. L. Newcomb, published in 1929,[9] shows the principal sources of about 225 vegetable drugs. Of these about 100 are credited to the United States, and only 13 to the whole of Mexico and Central America. But in Standley's Flora of Yucatan about 150 wild plants (counting groups of two or more closely related species as one) are said to have medicinal properties; and one might venture the guess that at least half of those have some real value.

Drugs of more or less importance are yielded by 15 large trees, 36 small trees, 8 woody vines, 20 shrubs, and 75 herbs. Among the most important are *Myroxylon Pereirae* (balsam of Peru), *Guaiacum sanctum* (lignum vitae), *Asclepias Curassavica* (milkweed), *Capsicum annuum* (red pepper), *Chenopodium ambrosioides* (wormseed), and *Datura* spp. (stramonium). In temperate regions more medicines come from roots and tubers than from the above-ground parts of plants, but in the tropics bark, leaves, flowers and seeds are used more. In Yucatan, as in the tropics generally, there seem to be more drug plants in the Leguminosae than in any other family.

In connection with drugs, poisonous plants deserve mention, though some of course are anything but useful. Those whose sap is poisonous to the skin are *Hippomane Mancinella* (manchineel), *Hura crepitans* (sandbox tree), *Gymnanthes lucida* (these three all in the Euphorbiaceae), and *Metopium Brownei* (Anacardiaceae).

Internal poisons include the roots of *Zamia furfuracea* (camotillo)[10] and *Manihot esculenta* (cassava), and the seeds of *Abrus*, *Erythrina*, and *Karwinskia*. Curiously enough, the roots of both *Zamia* and *Manihot* contain an abundance of starch, and are used for food after the poison is destroyed by heat.

*Gliricidia sepium*, a small leguminous tree, is sometimes used for

[9] See Torreya **30**: 74–77. June, 1930.

[10] The identity of camotillo seems to have been somewhat of a mystery. Standley does not give this common name in his Flora of Yucatan, but he does in his Flora of the Lancetilla Valley, Honduras, published a few months later. (Field Mus. Publ. 283, pp. 84–85. Jan., 1931.) Dr. Ralph H. Cheney, in recent papers on arrow-poisons (Sci. Monthly **23**: 554, 1926; Am. Jour. Bot. **18**: 138, 139, 1931) mentions camotillo as a plant reputed to be deadly, but does not identify it botanically. A recent newspaper syndicate feature mentions a Brazilian plant that is said to cause instant death to any one who touches it, and the picture accompanying it shows a plant which may very well be a *Zamia*. But the story is of course greatly exaggerated, for otherwise no botanist who attempted to classify the plant would have lived to complete his description.

poisoning rats and mice (whence its generic name), and two trees, *Piscidia* and *Hura*, and a woody vine, *Paullinia Cururu* (and related species) for poisoning fish.[11]

About half a dozen species of small trees, vines and herbs, of various families (especially Euphorbiaceae), are armed with nettle-like stinging hairs. The unwary explorer may get a dose of formic acid in another way, from two species of *Acacia* with hollow thorns, and species of *Cecropia* and *Cordia* with hollow twigs, which are inhabited by ants that rush out to attack anything that brushes against the plants or tries to climb them. Many similar cases (known as myrmecophilous plants) are known in other tropical countries.

### CHICLE GUM

*Achras Zapota* is one of the most abundant and useful large trees in Yucatan. It is planted for shade, its wood is useful for many purposes, it is cultivated (in Florida as well as in the tropics) for its edible fruit (sapodilla), and it is the source of chicle gum of which hundreds of tons are exported from Quintana Roo every year. The gum was known to the ancient Mayas, but its use in chewing gum in the United States is a comparatively recent development. It is gathered chiefly by the Maya Indians in the dense forests in the southeast, by primitive and wasteful methods, and the supply is said to be already seriously depleted.[12]

### DYES

Dyes come from about eight species, mostly trees and shrubs, and also from the cochineal insect, which feeds on a cultivated cactus. The most important dye wood is *Haematoxylum Campechianum*, the logwood, a small crooked leguminous tree. It was an important article of commerce as early as the 16th century, but has now been partly supplanted by aniline dyes. It also has astringent properties, recognized in the U. S. Pharmacopoeia. *Chlorophora tinctoria*, a small tree of the Moraceae, is the fustic of commerce, and yields yellow, brown and green dyes, which are used for dyeing khaki cloth.

### OTHER PRODUCTS

Other products of a chemical nature from wild plants are charcoal from *Gymnopodium antigonoides*, a small tree or shrub of the Polygonaceae, rub-

[11] For a recent study of mymecophilous plants, mostly from northern South America, see H. A. Gleason. The relationships of certain mymecophilous melastomes. Bull. Torrey Club **58**: 73–85. 1931.

[12] The process of gathering it is described in detail in an account copied from an English publication, in Tropical Woods (New Haven) **24**: 35–38. Dec. 1930.

ber from *Castilla elastica* and *Ficus cotinifolia* (Moraceae), gums and resins from *Bursera Simaruba*, *Myroxylon Pereirae* and *Protium Copal*, starch from roots of *Zamia*, *Maranta* and *Manihot*, oil from seeds of *Attalea Cohune* (a palm) and *Jatropha Curcas*, soap from the berries of *Sapindus Saponaria*, and tannin from the bark of *Pithecolobium albicans* and *Rhizophora Mangle*.

Cosmetics are obtained from *Rhoeo discolor* (Commelinaceae) and *Calocarpum mammosum* (Sapotaceae), and perfume from *Acacia Farnesiana*.

Other miscellaneous plant products are the leaves of *Cordia dodecandra*, used for sandpaper, water vessels from the fruits of *Crescentia Cujete* (calabash tree), toys from the pods of *Pithecoctenium*, and whistles from the stems of *Jatropha Gaumeri*.

UNIVERSITY, ALABAMA

# A list of algae from Missouri

FRANCIS DROUET

(WITH PLATES 18, 19)

The following list of species of algae is based on my collections in various parts of the state of Missouri during the past three years, and includes also any herbarium specimens of Missouri algae which have been called to my attention.

Several lists of algae have been reported from the state, all but one of which are from the Missouri Botanical Garden at St. Louis, by Hayden (1910), Spargo (1913), Moore and Karrer (1919), and Moore and Carter (1926). Few preserved specimens to support these identifications have been found. Many species appear in these lists which do not appear in my collections. Drouet (1930) reported 108 species from the vicinity of Columbia. These specimens have all been re-examined and are included in the present paper, which is intended to supplant, not to supplement, that of 1930.

The algal flora of Missouri is similar to that of the states bordering it. The state as a whole is not a definite geographical region; but, within its boundaries, three types of country can be distinguished.

The northern part of the state is glaciated and possesses a deep soil covering the underlying limestone. The streams are muddy for at least part of the year. Diatoms and species of *Cladophora* are the most abundant algae of these streams.

The southeastern part of the state is the low flood plain of the Mississippi and St. Francois Rivers. Drainage canals and shallow pools of standing water are characteristic. These bodies of water have been inadequately investigated. It appears, however, from my meager observations, that the algal vegetation is similar to that of ponds and shallow lakes throughout the state.

The Ozark or southern portion of the state is a rugged, hilly plateau with a maximum elevation of 1800 feet in Iron County. Clear, swift brooks flow over limestone and sandstone beds to the north, east, and south. These streams contain quantities of *Cladophora* spp., associated with diatoms and Zygnematables. In Gravois Creek, *Batrachospermum virgatum* forms an integral part of the submerged vegetation. This part of the state is peculiarly characterized by the presence of underground rivers which gush out of the earth as enormous springs. Big Spring, the largest of these, located in Carter County, discharged 223,000,000 gallons of water in one day, as measured by Rodhouse (1920) by means of a Price current meter. Rodhouse considers that the temperature of each of these large springs

remains at approximately 58°–60° F. during the entire year. The springs and their spring branches support in the spring and summer months a large subaquatic vegetation of *Rhizoclonium hieroglyphicum*, *Tribonema bombycinum*, *Lysigonium* sp., *Microspora Loefgrenii*, and *M. amoena*. Species of *Batrachospermum* occur in Bennett, Maramec, Gravois, Yancy Mills, and Round Springs. The subaërial algae are chiefly of species of *Vaucheria* and *Phormidium*. Representatives of the Oedogoniales, Desmidiaceae, Chlorococcales, and of the genus *Cladophora* are notably absent. In Maramec and Gravois Springs, a winter submerged association of vegetative *Vaucheria*, *Spirogyra*, and diatoms has been observed to replace the spring and summer vegetation.

A transitional region existing between the northern and Ozark areas includes the Missouri River valley and is characterized by the presence of clear or muddy streams and of numerous small springs. Some of these springs contain dissolved salts of iron and sulfur. At Chouteau Springs in Cooper County, hydrogen sulfide bubbles continuously through the water which issues from the springs. The retaining tiles are covered below the surface of the water with layers of *Oscillatoria chalybea*, *O. minima*, and sulfur bacteria. In the winter the tiles were found to be lined with *Calothrix parietina*, *Gloeocapsa* sp., and sulfur bacteria. The marsh through which the waters flow is covered with mats of *Enteromorpha intestinalis*. Small freshwater springs contain the usual submerged forms of *Stigeoclonium*, *Draparnaldia*, Zygnematales, *Tribonema*, and diatoms and the subaërial *Vaucheria* spp.

Artificial lakes, ponds, and smaller bodies of water contain the subaquatic species of *Pithophora*, Oedogoniales, Zygnematales, Chlorococcales, flagellates, and a variety of other groups. Desmids are usually few in both diversity of forms and number of individuals. Large bodies of water are rare in Missouri; the largest is the new Lake of the Ozarks in the valley of the Osage River. Our present knowledge of the algae of the submerged area furnishes a possibility of much interesting work on the origin and development of the vegetation of a large body of water.

Approximately 900 collections of algae have been preserved. The majority of these come from the central and southern parts of the state.

Collected material was examined in the living condition or in a 5 per cent aqueous solution of formalin. Each collection was then preserved in a small vial of 5 per cent aqueous formalin or of Pfeiffer's solution, as recommended by Hazen (1902). All of these vials are in my possession. Many specimens were dried and placed in the Herbarium of the University of Missouri. Specimens were identified according to the descriptions and keys in the large taxonomic works cited at the end of this paper; and,

as far as possible, these descriptions were compared with original diagnoses of species. Most of the specimens were compared with exsiccatae in the Phycotheca Boreali-americana and the American Algae. Dr. William Randolph Taylor, Dr. Gilbert Morgan Smith, and Dr. Tracy E. Hazen were so kind as to examine a few of the specimens. The exsiccatae from Missouri in the Herbarium of the Missouri Botanical Garden and plankton collections made by the U. S. Bureau of Fisheries from the Mississippi River bordering Missouri were also examined and are included in the list.

The Desmidiaceae and the flagellate groups have been identified, at least approximately, by the use of standard monographic keys and descriptions; but the lists of species of these groups are intended more to show the variety of such organisms within the state than to extend the knowledge or distribution of individual species.

I wish here to express my appreciation to Dr. H. W. Rickett and other members of the Department of Botany and to Dr. W. R. Taylor of the University of Michigan for guidance and kindly criticism during the progress of this work; to Dr. G. T. Moore and Dr. J. M. Greenman for the use of the library and herbarium at the Missouri Botanical Garden; to Miss Ada Hayden for the loan of her original sketches of Missouri algae; to Dr. M. M. Ellis for the use of the collections of the U. S. Bureau of Fisheries; and to the many interested people who were so kind as to collect specimens for me.

## LIST OF SPECIES

The scheme of classification used here is based upon that of West and Fritsch (1927) and of Fritsch (1929), supplemented by that of the authors of Pascher's *Süsswasserflora*. Distribution of forms within the state is indicated by the names of counties following each citation. Names of collectors appear in italics.

## CHLOROPHYCEAE

### VOLVOCALES

Chlamydomonas communis Snow. Boone.
Chlamydomonas gracilis Snow. Boone.
Polytoma uvella Ehr. Boone.
Gonium pectorale Müll. Boone.
Pandorina Morum Bory. Boone (*Schmidt*), St. Clair.
Eudorina elegans Ehr. Boone, Lewis (*Ellis*).
Eudorina illinoisensis (Kofoid) Pascher. Mississippi.
Platydorina caudata Kofoid. Camden.
Sphaerella lacustris (Gir.-Chantr.) Wittr. Mississippi.
Volvox sp. Boone (*Holtzwart*).

## TETRASPORALES

GLOEOCYSTIS FENESTRALIS (Kütz.) A. Br. St. Louis (*Collins*).
TETRASPORA GELATINOSA (Vauch.) Desv. Jackson, Boone.
TETRASPORA LUBRICA (Roth) Ag. Boone, Lawrence (*Leake*).
TETRASPORA spp. Boone, Monroe.

## CHLOROCOCCALES

CHLOROCOCCUM HUMICOLUM (Näg.) Rab. Boone.
CHARACIUM BRAUNII Bruegger var. Boone. (*Fig. 1.*)

This form is somewhat smaller than the type but seems to correspond with the latter in the shape of the cell. Our plants measure 23–27$\mu$ long and 3–7$\mu$ wide.

CHARACIUM FALCATUM Schroeder. Boone.
CHLOROCHYTRIUM LEMNAE Cohn. Boone (*M. Johnson*).
PEDIASTRUM BORYANUM (Turp.) Men. Cooper.
PEDIASTRUM DUPLEX Meyen. Clay (*Elmore*), Lewis (*Ellis*), Mississippi.
PEDIASTRUM TETRAS (Ehr.)Ralfs. Boone, Mississippi.
HYDRODICTYON RETICULATUM (L.) Lag. Boone, St. Louis (*Pfeiffer, Hayden*).
CHLORELLA VULGARIS Beijerinck. Boone, Cooper, Maries.
ACANTHOSPHAERA ZACHARIASII Lemm. Boone.
OOCYSTIS LACUSTRIS Chodat. Cooper.
LAGERHEIMIA CITRIFORMIS (Snow) G. M. Smith. Mississippi.
TETRAEDRON LONGISPINUM (Perty) Hansg. Boone.
TETRAEDRON MINIMUM (A. Br.) Hansg. Boone.
TETRAEDRON MUTICUM (A. Br.) Hansg. Mississippi.
TETRAEDRON QUADRATUM (Reinsch) Hansg. Boone.
KERATOCOCCUS RHAPHIDIOIDES (Hansg.) Pascher. Boone.
ANKISTRODESMUS FALCATUS (Corda) Ralfs. Boone.
A. FALCATUS ACICULARIS (A. Br.) G. S. West. Boone.
A. FALCATUS SPIRILLIFORMIS G. S. West. Boone, Grundy (*Cunningham*), Hickory, Osage.
ANKISTRODESMUS LONGISSIMUS (Lemm.) Wille. Boone.
SELENASTRUM GRACILE Reinsch. Howard (*Petry*).
SELENASTRUM MINUTUM (Näg.) Collins. Mississippi, St. Clair.
DICTYOSPHAERIUM EHRENBERGIANUM Näg. Boone.
SCENEDESMUS ACUMINATUS MINOR G. M. Smith. Montgomery.
SCENEDESMUS ARMATUS (Chod.) G. M. Smith. Mississippi.
SCENEDESMUS BIJUGA (Turp.) Lag. Howell, Boone.
SCENEDESMUS CARINATUS (Lemm.) Chod. Hickory.
SCENEDESMUS DIMORPHUS (Turp.) Kütz. Caldwell (*Elmore*), Lewis (*Geisendorfer*), St. Clair, Montgomery.
SCENEDESMUS OBLIQUUS (Turp.) Kütz. Henry.
SCENEDESMUS OPOLIENSIS Richter. Clay (*Elmore*).
SCENEDESMUS QUADRICAUDA (Turp.) Breb. Boone, Lewis (*Geisendorfer*), Mississippi.
COELASTRUM MICROPORUM Näg. Boone, Cooper, Audrain, Mississippi, St. Clair, Vernon.

## ULOTRICHALES

ULOTHRIX TENERRIMA Kütz. Boone, Lewis (*Geisendorfer*).
HORMIDIUM FLACCIDUM A. Br. *sens. ampl.* Boone, Pulaski.

STICHOCOCCUS SCOPULINUS Hazen. Boone (*Glen Huff*).

CYLINDROCAPSA GEMINELLA MINOR Hansg. Boone.

ENTEROMORPHA INTESTINALIS (L.) Grev. f. TENUIS Collins. Cooper. (*Figs. 2, 3.*)

This form has been observed only in a marsh supplied with salt water containing dissolved hydrogen sulfide at Chouteau Springs in Cooper County. Collins (1909) points out that the plants may be the same as *E. intestinalis crispa* Ktz., but that Kützing has given an insufficient description for the variety. The type specimen of the forma *tenuis* is No. 125 of Tilden's American Algae, collected in 'artesian, running water' in South Dakota.

MICROSPORA AMOENA (Kütz.) Rab. Camden, Phelps, Morgan.

This species and the next are found only in those collections from the large springs of the Ozarks.

MICROSPORA LOEFGRENII (Nordst.) Lag. Phelps, Pulaski.

MICROSPORA QUADRATA Hazen. Boone.

MICROSPORA STAGNORUM (Kütz.) Lag. Boone, Cooper, St. Louis (*Collins*).

MICROSPORA TUMIDULA Hazen. Boone, Hickory.

STIGEOCLONIUM LUBRICUM (Dillw.) Kütz. Dallas.

STIGEOCLONIUM TENUE (Ag.) Kütz. Boone, Jackson.

STIGEOCLONIUM spp. Jackson, Randolph, Monroe, Grundy (*Cunningham*).

DRAPARNALDIA ACUTA (Ag.) Kütz. Boone, Monroe, Hickory.

DRAPARNALDIA GLOMERATA (Vauch.) Ag. Boone.

DRAPARNALDIA PLUMOSA (Vauch.) Ag. Boone, Dallas, Cooper.

CHAETOPHORA ELEGANS (Roth) Ag. Boone, Reynolds, Lawrence (*Leake*).

CHAETOPHORA INCRASSATA (Huds.) Hazen. Boone, Miller, Morgan.

CHAETOPHORA PISIFORMIS (Roth) Ag. Boone.

MICROTHAMNION KUETZINGIANUM Näg. Boone.

MICROTHAMNION STRICTISSIMUM Rab. Clay (*Elmore*), Audrain, Callaway.

PROTODERMA VIRIDE Kütz. Dent, Marion (*Gulick*).

APHANOCHAETE REPENS A. Br. Boone, Grundy (*Cunningham*), Miller, St. Clair, St. Charles (*Ennis*), Ralls (*Gulick*).

PLEUROCOCCUS NAEGELII Chod. Boone, Jackson, Pemiscot (*Miller*), Cooper, Barry (*Leake*), Carroll (*Elmore*).

## CLADOPHORALES

RHIZOCLONIUM HIEROGLYPHICUM (Ag.) Kütz. Boone, Camden, Shannon, Carter, Reynolds, Clay (*Elmore*), Pulaski, Benton, St. Clair, Johnson, Montgomery, Miller, Barry (*Leake*), Stone (*Leake*), Morgan, St. Louis (*Collins*).

CLADOPHORA CRISPATA (Roth) Kütz. ampl. Brand. Jackson, St. Francois (*Nahm*), Cole, Vernon, Caldwell (*Old*).

CLADOPHORA FRACTA (Dillw.) Kütz. ampl. Brand. St. Charles (*Ennis*), Ralls (*Gulick*), Montgomery.

CLADOPHORA GLOMERATA (L.) Kütz. ampl. Brand. Cooper, Boone, Camden, St. Clair (*H. F. Hand*), Jackson, St. Louis Co. (*Nelson, Holtzwart*), Miller, Clay (*Elmore*).

PITHOPHORA MOOREANA Collins. St. Louis (Moore).

PITHOPHORA OEDOGONIA (Mont.) Wittr. Boone, St. Louis (*Hayden*).

PITHOPHORA VARIA Wille. Clay (*Elmore*).

## OEDOGONIALES

BULBOCHAETE sp. Boone.
OEDOGONIUM CAPILLIFORME (Kütz.) Wittr. St. Louis (*Pammel*).
OEDOGONIUM INTERMEDIUM Wittr. Dent, Howell.
OEDOGONIUM MARTINICENSE Hirn. Boone.
OEDOGONIUM PISANUM Wittr. Jackson.
OEDOGONIUM RUFESCENS Wittr. Audrain.
OEDOGONIUM spp. Common.

## ZYGNEMATALES

ZYGNEMA INSIGNE (Hass.) Kütz. Boone.
ZYGNEMA STELLINUM (Müll.) Ag. Platte (*Holtzwart*), Jackson, Randolph (*Adams*).
ZYGNEMA (?) PECTINATUM (Vauch.) Ag. Moniteau.
SPIROGYRA AFFINIS (Hass.) Petit. Jackson (*J. & R. R. Drouet*).
SPIROGYRA BELLIS (Hass.) Cleve. Callaway.
SPIROGYRA COMMUNIS (Hass.) Kütz. Boone.
SPIROGYRA DECIMINA (Müll.) Kütz. Boone, Camden, Grundy (*Cunningham*).
SPIROGYRA ELLIPSOSPORA Transeau. Boone.
SPIROGYRA FLUVIATILIS Hilse. Boone, Miller.
SPIROGYRA GRACILIS (Hass.) Kütz. Jackson (*J. & R. R. Drouet*).
SPIROGYRA GREVILLEANA (Hass.) Kütz. Boone, Jackson (*J. & R. R. Drouet*).
SPIROGYRA IRREGULARIS Näg. Cedar.
SPIROGYRA JUERGENSII (Kütz.) Petit. Jackson.
SPIROGYRA LONGATA (Vauch.) Kütz. Reynolds.
SPIROGYRA PORTICALIS (Müll.) Cleve. Boone, Audrain.
SPIROGYRA SUBMAXIMA Transeau. Grundy (*Cunningham*).
SPIROGYRA VARIANS (Hass.) Kütz. Grundy (*Cunningham*).
SPIROGYRA WEBERI (Kütz.) Petit. Boone.
MOUGEOTIA VIRIDIS (Kütz.) Wittr. Mississippi.
PENIUM LIBELLULA (Focke) Nordst. Boone.
PENIUM MARGARITACEUM (Ehr.) Breb. Boone, Hickory.
CLOSTERIUM ACEROSUM (Schrank.) Ehr. Boone.
CLOSTERIUM LANCEOLATUM Kütz. Boone, Benton.
CLOSTERIUM LEIBLEINII Kütz. Callaway, Boone, Benton, Henry
CLOSTERIUM MONILIFERUM (Bory) Ehr. Boone, Camden, Jackson, Grundy (*Cunningham*), Pulaski, St Clair.
CLOSTERIUM PERACEROSUM G. S. West. Boone.
CLOSTERIUM PRITCHARDIANUM Arch. Boone.
CLOSTERIUM SUBTRUNCATUM W. & G. S. West. Boone, Morgan.
PLEUROTAENIUM MAXIMUM (Reinsch) Lund. Dent.
PLEUROTAENIUM TRUNCATUM (Breb.) Näg. Boone.
COSMARIUM UNDULATUM Corda. Dallas.
COSMARIUM spp. Common.
HYALOTHECA MUCOSA (Dillw.) Ehr. Randolph (*Adams*), Morgan, Ralls (*Gulick*).
DESMIDIUM SWARTZII Ag. Marion (*Gulick*).

## SIPHONALES

VAUCHERIA AVERSA Hass. Randolph (*Adams*).
VAUCHERIA GEMINATA (Vauch.) DC. Boone, Jackson, Randolph (*Adams*), Miller, Marion (*Gulick*), Caldwell (*Old*).

VAUCHERIA ORTHOCARPA Reinsch. Cass (*J. & R. R. Drouet*), Grundy (*Cunningham*).
VAUCHERIA POLYSPERMA Hass. Boone, Callaway.
VAUCHERIA REPENS Hass. Dent, Benton, Johnson, Cole, St. Louis (*Collins*).
VAUCHERIA SESSILIS (Vauch.) DC. Shannon, Boone.
VAUCHERIA spp. Common.

## HETEROKONTAE

BOTRYOCOCCUS BRAUNII Kütz. Boone, Vernon.
CHLOROBOTRYS REGULARIS (West) Bohlin. Boone.
TRIBONEMA BOMBYCINUM (Ag.) Derb. & Sol. Jackson, Howard, Phelps, Pulaski, Grundy (*Cunningham*), Morgan, Ralls (*Gulick*), Stone (*Leake*), Boone.
f. TENUE Hazen. With *T. bombycinum*.
TRIBONEMA MINUS (Wille) Hazen. Boone, Dent, Morgan.
BOTRYDIUM GRANULATUM Grev. Boone, Howard (*Petry*).

## CHRYSOPHYCEAE

DINOBRYON SOCIALE Ehr. Iron.

## CRYPTOPHYCEAE

CHILOMONAS PARAMOECIUM Ehr. Boone.

## DINOPHYCEAE

CERATIUM HIRUNDINELLA O. F. M. Boone.

## EUGLENINEAE

EUGLENA ACUS Ehr. Howell.
EUGLENA DESES Ehr. Boone, Callaway.
EUGLENA ELONGATA Schew. Boone.
EUGLENA OXYURIS Schmarda. Boone.
EUGLENA PISCIFORMIS Klebs. Boone.
EUGLENA SANGUINEA Ehr. Boone, Reynolds, St. Louis?
EUGLENA SPIROGYRA Ehr. Boone, Benton.
EUGLENA SPIROIDES Lemm. Boone.
PHACUS PLEURONECTES (O. F. M.) Duj. Boone, Cooper, St. Clair, Morgan.
PHACUS LONGICAUDA (Ehr.) Duj. Boone, Howell.
TRACHELOMONAS ELEGANS Conrad. Lewis (*Geisendorfer*).
TRACHELOMONAS VOLVOCINA Ehr. Boone.
TRACHELOMONAS HISPIDA (Perty) Defl. Boone.

## RHODOPHYCEAE

PORPHYRIDIUM CRUENTUM (Ag.) Näg. Boone, St. Louis (*Norton, Collins*).
BATRACHOSPERMUM BÓRYANUM Sirdt. *Identification by Wm. R. Taylor.* Phelps.
BATRACHOSPERMUM VIRGATUM (Kütz.) Sirdt. *Identification by Wm. R. Taylor.* Morgan.
BATRACHOSPERMUM spp. Dallas, Stone (*Leake*), Phelps, Shannon.

## MYXOPHYCEAE

### CHROOCOCCALES

MICROCYSTIS AERUGINOSA Kütz. Johnson.

APHANOCAPSA ELACHISTA W. & G. S. West. Cooper, Boone.

APHANOTHECE SAXICOLA Näg. St. Clair.

This form covers the rocks and ironwork about a spring in which hydrogen sulfide bubbles. It has been found in Missouri only at Monegaw Springs.

GLOEOCAPSA FUSCO-LUTEA (Näg.) Rab. Boone (*Petry*).

GLOEOTHECE LINEARIS Näg. St. Louis (*Collins*).

CHROOCOCCUS MINOR (Kütz.) Näg. Boone, Clay (*Elmore*), St. Clair.

CHROOCOCCUS MINUTUS (Kütz.) Näg. Boone, Morgan.

CHROOCOCCUS REFRACTUS Wood. Boone, St. Louis Co. (*Holtzwart*).

CHROOCOCCUS TURGIDUS (Kütz.) Näg. Boone, St. Louis Co. (*Holtzwart*), Benton, St. Francois (*Mosier*), Cooper.

CHROOCOCCUS TURICENSIS (Näg.) Hansg. Montgomery.

COELOSPHAERIUM NAEGELIANUM Ung. St. Charles (*Ennis*), Johnson. (*Fig. 4.*)

MERISMOPEDIA CONVOLUTA Breb. Cooper.

MERISMOPEDIA ELEGANS A. Br. Johnson.

MERISMOPEDIA GLAUCA (Ehr.) Näg. Dallas, Howell, Shannon, Boone, Texas, Benton, Johnson.

MERISMOPEDIA TENUISSIMA Lemm. Boone, Benton.

### CHAMAESIPHONALES

CNCOBYRSA RIVULARIS (Kütz.) Geitler. Morgan.

CHAMAESIPHON INCRUSTANS Grun. Camden, Pulaski, Stone (*Leake*).

### HORMOGONALES

SPIRULINA MAJOR Kütz. Franklin (*Holtzwart*), Henry, St. Clair, Randolph (*Adams*).

SPIRULINA NORDSTEDTII Gomont. Boone.

OSCILLATORIA AGARDHII Gomont. Reynolds, St. Louis (*Hus*).

OSCILLATORIA AMOENA (Kütz.) Gomont. Boone, St. Clair, Hickory, Cooper, Pettis.

OSCILLATORIA ANGUINA (Bory) Gomont. Boone, Miller, Lewis (*Geisendorfer*), Grundy (*Cunningham*).

OSCILLATORIA ANGUSTISSIMA W. & G. S. West. Boone, Jackson.

OSCILLATORIA BREVIS Kütz. Boone, Pulaski.

OSCILLATORIA CHALYBEA Mertens. Cooper.

OSCILLATORIA CURVICEPS Ag. Randolph (*Adams*). (*Fig. 5.*)

The trichomes of our material are 6.4–10$\mu$ wide, whereas those of the type are 10–17$\mu$ wide.

OSCILLATORIA FORMOSA Bory. Boone, Jackson, Howard, Randolph (*Adams*).

OSCILLATORIA LIMOSA Ag. Boone, Camden, Cooper Saline.

OSCILLATORIA MINIMA Giklhorn. Cooper. (*Fig. 6.*)

This alga grows, as Geitler (1925) points out, in water containing dissolved hydrogen sulfide. At Chouteau springs, the trichomes are associated with *O. chalybea* and sulfur bacteria. With dark field illumination, the trichomes reflect blue light. This phenomenon of *Blauglanz* Geitler says is characteristic of certain Oscillatorias of sulfur springs.

OSCILLATORIA ORNATA Kütz. Miller, Boone, St. Clair, Montgomery.

OSCILLATORIA PRINCEPS Vauch. Howell, Mississippi, Boone, Morgan, Benton, St. Louis (*Webber*), Dunklin (*Trelease*).

OSCILLATORIA PROBOSCIDEA Gomont. Camden, Shannon.

OSCILLATORIA SPLENDIDA Grev. Howell, Boone, Randolph (*Adams*), Miller, Morgan, St. Clair, Benton, Pettis, Cooper.

OSCILLATORIA SUBTILISSIMA Kütz. Boone, Morgan, Johnson.

OSCILLATORIA TENUIS Ag. Boone, Howell, 'Spring Park' (*F. W. D.*), Dunklin (*Trelease*).

O. TENUIS NATANS Kütz. Boone, Morgan.

O. TENUIS TERGESTINA (Kütz.) Rab. Howell, Shannon, Boone, Randolph (*Adams*).

PHORMIDIUM AUTUMNALE (Ag.) Gomont. Boone, Camden, Monroe, Clay (*Elmore*), Pulaski, Morgan, Stone (*Leake*).

PHORMIDIUM FOVEOLARUM (Mont.) Gomont. Scott, Lewis (*Geisendorfer*).

PHORMIDIUM FRAGILE (Men.) Gomont. Boone.

PHORMIDIUM UNCINATUM (Ag.) Gomont. Phelps, Clay (*Elmore*), Randolph (*Adams*).

The small species of *Phormidium* and *Lyngbya* are often difficult to distinguish. The amount of confluence and diffluence of the sheaths is an uncertain criterion, especially since the volume and consistency of the sheath surely depend upon the internal condition of the protoplasm and upon the character of the environment. In this environment, bacteria which destroy the jelly are always present and are usually abundant. In Missouri, at least, the two genera are in need of critical examination, especially the smaller species.

LYNGBYA MARTENSIANA Men. Boone, St. Louis Co. (*Holtzwart*), Morgan, Cooper, Bates.

LYNGBYA OCHRACEA (Kütz.) Thuret. Boone.

LYNGBYA spp. Franklin (*Holtzwart*), Henry.

SYMPLOCA MUSCORUM (Ag.) Gomont. Boone, Johnson.

SCHIZOTHRIX sp. St. Clair.

HYDROCOLEUS RAVENELII Wolle. Boone.

MICROCOLEUS LACUSTRIS (Rab.) Farlow. Cooper, Henry, Montgomery.

MICROCOLEUS PALUDOSUS (Kütz.) Gomont. Boone.

MICROCOLEUS SOCIATUS W. & G. S. West. Cole, Moniteau. (*Fig. 7.*)

MICROCOLEUS VAGINATUS (Vauch.) Gomont. Boone, Miller, Henry, St. Clair, St. Charles (*Ennis*), Ralls (*Gulick*), Moniteau.

APHANIZOMENON FLOS-AQUAE (L.) Ralfs. Johnson, St. Louis Co. (*Holtzwart*).

Our material is all of the minimum dimensions described for the type and almost coincides with those of the Russian *A. Flos-aquae Klebahnii* Elenkin.

NOSTOC COMMUNE Vauch. Boone.

Although this alga has been collected from the same locality at least once a month for two years and has been repeatedly grown in the laboratory, no gonidia have been observed on it.

NOSTOC MUSCORUM Ag. Boone, Osage.

NOSTOC VERRUCOSUM (L.) Vauch. Phelps, Dent.

ANABAENA CATENULA (Kütz.) Born. & Flah. St. Louis (*Hunt*).

ANABAENA HALLENSIS (Jancz.) Born. & Flah. Boone.

ANABAENA INAEQUALIS (Kütz.) Born. & Flah. Grundy (*Cunningham*), Jackson, Boone, Callaway. (*Fig. 8.*)

Tilden (1910) has noted in her diagnosis of this species that the gonidia are

remote from the heterocysts; but her figures show them also contiguous to the heterocysts, as in our specimens.

ANABAENA TORULOSA (Carm.) Lag. Mississippi.

(?) ANABAENA sp. Shannon. (*Fig. 9.*)

The trichomes of this material are devoid of heterocysts and gonidia, but the shapes of the cells and the habit of the plants make it plausible to call the form an *Anabaena*. Whether or not the material represents a new species of *Pseudanabaena* must be learned by future collecting.

CYLINDROSPERMUM MAJUS Kütz. Boone, Jackson.

PLECTONEMA WOLLEI Farlow. St. Louis Co. (*Holtzwart*).

SCYTONEMA MIRABILE (Dillw.) Born. Montgomery.

SCYTONEMA OCELLATUM Lyngb. Boone, St. Louis (*Collins*).

TOLYPOTHRIX TENUIS Kütz. Randolph (*Adams*).

HOMOEOTHRIX ENDOPHYTICA Lemm. Morgan. (*Fig. 10.*)

I have found no previous record of *Homoeothrix* in America; but the conspicuous absence of heterocysts and the striking agreement of the habit and form of the filaments with the description by Geitler (1925) force me to call this alga *H. endophytica*. It differs from *Calothrix fusca* (Kütz.) Born. & Flah. in the width of the sheaths and in the absence of heterocysts. The specimens have cells 6–9$\mu$ wide and 1.5–2$\mu$ long at the middle and base of the trichome, and they are imbedded in the thalli of *Batrachospermum virgatum* from the spring branch at Gravois Mills, Morgan Co.

CALOTHRIX BRAUNII Born. & Flah. Cooper.

CALOTHRIX CASTELLII (Massal.) Born. & Flah. Hickory.

CALOTHRIX PARIETINA (Näg.) Thuret. Boone, Cooper.

RIVULARIA sp. Boone.

DEPARTMENT OF BOTANY
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## Explanation of plates

### PLATE 18

Photographs by Dr. H. W. Rickett.

Fig. 1. Big Spring in Carter County, near Van Buren. This is the largest spring in Missouri. Notice the enormous volume of water which issues from such a spring.

Fig. 2. The lower spring branch of Maramec Spring, six miles southeast of St. James in Phelps County. This spring, according to Rodhouse (1920), discharged 88,000,000 gallons of water in one day. Notice the excellent algal habitats along the edge of the brook. The conspicuous vegetation consists mostly of *Radicula Nasturtium-aquaticum*.

### PLATE 19

These figures were made with the aid of a Bausch and Lomb camera lucida and a Bausch and Lomb binocular microscope with various combinations of the 6×, 10×, and 25× oculars and the 16 mm., 4 mm., and 1.9 mm. objectives.

Fig. 1. *Characium Braunii* var. ×1000.

Fig. 2. *Enteromorpha intestinalis* f. *tenuis*. Cross section of the cells of the frond. The inner membrane is on the left hand side. ×400.

Fig. 3. *Enteromorpha intestinalis* f. *tenuis*. Surface view of the cells. ×400.

Fig. 4. *Coelosphaerium Naegelianum*. a. Typical colony. ×150. b. Cells showing pseudovacuoles. ×600.

Fig. 5. *Oscillatoria curviceps*. ×400.

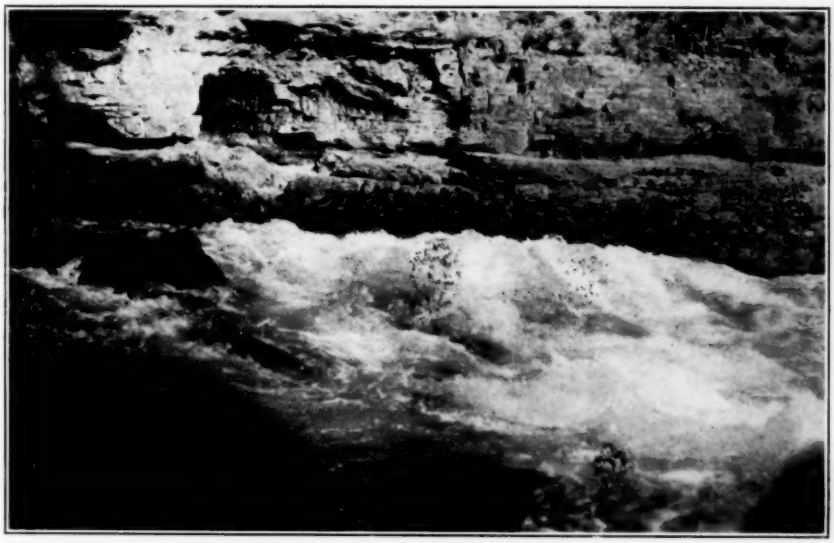
Fig. 6. *Oscillatoria minima*. ×1000.

Fig. 7. *Microcoleus sociatus*. Ends of two trichomes. ×1000.

Fig. 8. *Anabaena inaequalis*, showing gonidia contiguous to a heterocyst. ×1000.

Fig. 9. (?) *Anabaena* sp. ×1000.

Fig. 10. *Homeothrix endophytica*. a. A filament and a trichome. ×350. b. Detail of cells of a trichome. ×1500.



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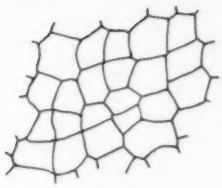

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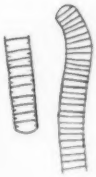

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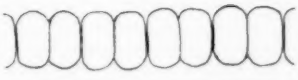

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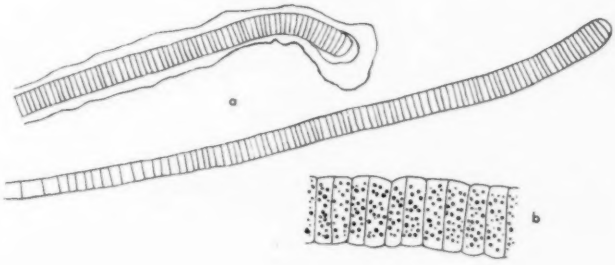


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## INDEX TO AMERICAN BOTANICAL LITERATURE

### 1928–1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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